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# SOME POINTS IN THE CRANIAL DEVELOPMENT OF TELEOSTOMIAN FISHES

D I S S E R T A T I O N  
FOR THE DOCTORATE  
PRESENTED TO THE FACULTY  
OF SCIENCE IN STOCKHOLM  
AND PUBLICLY MAINTAINED  
APRIL 8<sup>TH</sup> TO A. M. IN  
THE ZOOTOMICAL INSTITUTE



BY

TORSTEN PEHRSSON  
L. L. PHIL.

STOCKHOLM  
ALB. BONNIERS BOKTRYCKERI  
1922

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# SOME POINTS IN THE CRANIAL DEVELOPMENT OF TELEOSTOMIAN FISHES.

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*TORSTEN PEHRSON.*

With 24 figures in the text.

## INTRODUCTION.

The embryonic development of the skull of fishes has been investigated by a comparatively small number of workers. Some special problems, however, as for instance, the question of the origin of the occipital region and the metamery of the head, are thoroughly dealt with. But, on the other hand, the development of the entire skeleton of the head has been investigated only in a few species. Our knowledge of the development of the Selachian cranium is chiefly based on the works of PARKER and SEWERTZOFF. Amongst Ganoids only Chondrostei (PARKER, SEWERTZOFF) and Lepidosteus (PARKER, VEIT) have been examined. The Teleosts have naturally been treated by a large number of workers. The development of the whole cranium is known from the investigations of PARKER, STÖHR (*Salmo*), GAUPP, BÖKER (early stages in *Salmo*), McMURRICH (*Syngnathus*), SWINNERTON (*Gasterosteus*), UHLMANN (*Cyclopterus*), to mention only a few names. The development of the cranial bones has, some years ago, been very satisfactory examined by SCHLEIP (*Salmo*).

My original intention with the present paper was, by investigation of the embryonic development of the cranial bones in *Amia* to contribute towards the solution of the question of the derivation of the dermal bones, in particular of those related to the sensory canals.

In the literature, however, with the exception of papers treating of the occipital region, only isolated notices on the development of the primordial cranium in *Amia* are to be found. In consequence of this, I consider it suitable to give an account of the latter as well. In so doing, I have avoided expressing an opinion on questions of a more general nature touching the ontogeny of the cartilaginous cranium, such as those on the phylogeny of the cranium, the metamery of the head, etc., because they lie outside the scope of my work. For instance, I have not considered it necessary to treat with the metamery of the occipital region for the above-mentioned reasons, and also because *Amia* has, ever since SCUREINER, been the classical object of

these investigations. Neither have I treated the origin of the branchial skeleton, since it is of little interest from the main points of view of this work.

The constant relations between the sensory canals and certain bones of the cranium have long been well-known (comp. page 36). ALLIS, in particular, has by a serie of extremely valuable papers definitely established this fact, thereby enriching comparative morphological investigation with a singularly useful aid for homologizing the bones in question. ALLIS has likewise, in his studies on the development of the sensory canals in *Amia*, and on the anatomy of the head in the same fish, produced standard-works of the greatest value for every student of the structure or development of the head of fishes. In this connection I cannot omit pointing out that the contributions of this distinguished investigator have to a certain extent been neglected by German scientists (e. g. GAUPP).

In the course of my work it has proved possible to establish morphogenetic views, leading to satisfactory results, on the development of the cranial bones arising in connection with the sensory canals. This has been rendered possible mainly by the exceedingly good material for comparative study of fossil Teleostomes found in STENSIÖ's paper "Triassic Fishes from Spitzbergen".

It is my intention in a future work to treat the development of the remaining bones of the cranium as well.

My investigations have been carried out at the Zootomical Institute of the Stockholms Högskola. The necessary material has been kindly placed at my disposal by Professor NILS HOLMGREN, to whom it is a pleasant duty to express my hearty thanks, not only for his valuable suggestion for this paper, but also for the good advice and kind interest he has invariably shown me during the course of my work.

#### MATERIAL AND METHOD.

The following embryonic stages have been investigated. The body-length is measured after fixation.

##### *Amia calva.*

Stage	1.	Total length	7,5	mm.	Stage	8.	Total length	12	mm.
"	2.	"	8,0	"	"	9.	"	13,6—14	"
"	3.	"	8—8,8	"	"	10.	"	19,5	"
"	4.	"	9,3	"	"	11.	"	21,5	"
"	5.	"	9,2—9,9	"	"	12.	"	31,5—34,5	"
"	6.	"	10—11	"	"	13.	"	56	"
"	7.	"	10,6	"					

*Polypterus*. Total length 35 mm. and 125 mm.

*Lepidostern*. Total length 70 mm.

I have generally examined series of transverse sections, stained with haemalum according to MAYER or haematoxylin according to F. C. C. HANSEN, contrastained with fuchsin S. The reconstructions are made after the graphic method of KASTSCHENKO.

## THE DEVELOPMENT OF THE PRIMORDIAL CRANIUM OF *AMIA CALVA*.

In the larval stages, immediately preceding those in which skeletal elements can be observed, the conditions in *Amia* in regard to the differentiation of the skeletal tissues agree with the data touching corresponding stages given e. g. by VEIT (1911) in regard to *Lepidosteus*, and by STÖHR (1882) in regard to *Salmo*. Thus the notochord and the brain are enclosed in a sparsely nucleated mesenchyma, in which those skeletal parts, which are preformed in the prochondrium, may be tolerably well delimited in so far as they exist. The space where the future visceral skeleton will develop is on the other hand filled with a densely nucleated tissue, in which the different elements can only be determined with certainty in later stages, when cartilage has already developed.

*Stage 1 and 2.* Total length 7.5—8 millimetres.

Instead of giving a description of the exterior of these as well as the following stages I beg to refer to ALLIS (1880) whose excellent pictures give sufficient information about the external development.

In the neural cranium cartilaginous trabeculae and parachordals have developed. The trabeculae extend in the shape of cylindrical rods, diverging somewhat caudad from the approximate of the opticus to the hypophysis. On each side of the hypophysis they pass into a cartilage plate (*Pp*) which is continued caudally by the more medially situated parachordals. The trabeculae extend as prochondrium rostrally as far forward as the front part of the eyes. Figs. 1 and 2, which represent a more advanced stage, give an idea of the appearance of the cranium.

VEIT (1911) describes in *Lepidosteus* a pair of independent cartilages, situated between the parachordals and the trabeculae, and in the rostral extension of the former. These cartilages he calls "Polknorpel" in accordance with the terminology of VAN WIJNE (1904), who found similar formations in *Acanthias*. Although such independent cartilages have not been found in *Amia*, their homologons are undoubtedly met with in the above mentioned lamelliform extensions (*Pp*) on the boundary between the trabeculae and the parachordals. *Musculus rectus lateralis bulbi* has, in fact, the same position in relation to these as to the "Polknorpel" of *Lepidosteus* and *Acanthias*.

It may be observed that the intercellular substance in the least advanced

specimen representing stage 1 is first formed in this plate. The development into cartilage then proceeds rostrally in the trabeculae and caudally in the parachordals.

The parachordals are in the form of two threesided rods with rounded edges, which stretch caudad along and close to the inside of the facial ganglion, which in these early stages is wholly detached from the trigeminus-ganglion, as is also the case in *Lepidosteus*. They then continue along and beneath the ganglion acusticum, which is attached to the facial ganglion. They are connected by a prochondral cellular bridge to the capsula acustica, which still remains prochondral. Behind the latter they begin to approach the notochord and increase in breadth, but at the same time losing their well-defined limits towards the surrounding mesenchyma. This posterior part of the parachordals has in fact not yet developed into real cartilage, but becomes farther caudad transformed into a tissue, which gradually assumes the nature of mesenchyma, lying close to the notochord. In the neighbourhood of the exit of the vagus this tissue takes on the same appearance as the surrounding mesenchyma. Each parachordal might thus be divided into one anterior pre-capsular part, which develops first independently of the notochord, and a posterior postcapsular part, which develops later and lies closer to the notochord. It is remarkable that so great a part of the notochord is unattached and only surrounded by indifferent mesenchyma, a fact which is still more evident in later stages.

In the visceral cranium the Meckelian cartilage may be observed at stage 2 in the shape of a pair of cylindrical cartilage rods, which proximate in the centre without, however, becoming fused. Each cartilage consists of one transverse median part, which passes laterally into a shorter and thicker caudally directed portion. The cartilage of Meckel is remarkably short during earlier embryonic development. The mandibula occupies a transverse position and resembles that of *Selachii*: the mouth being thus situated ventrally.

The Meckelian cartilage is united to the palato-quadrata by prochondrial tissue. The quadrata part resembling a flattened vertical plate, as well as a cylindrical projection extending from it, have become converted into cartilage. This projection is the rudiment of the pterygo-palatine part. Rostrally it changes gradually from prochondrium into a rather densely nucleated mesenchyma with indistinct boundaries. The mesenchymatous part lying close to the roof of the mouth cavity along a longitudinal ridge of teeth-rudiments appears partly attached to this ridge, without any well-defined boundary-line, — a condition which is also met with in Teleosts and which made LUNDBORG (1809) suggest an ectodermal derivation of the palato-quadrata. A similar longitudinal ridge of teeth-rudiments runs a little below each trabecula, but separated from it by ordinary mesenchyma. Perhaps an ancestral arrangement of the palatine teeth may be traced in this condition. The most frontal part

of the palato-quadrate has developed into typical prochondrium and joins the tips of the trabeculae without any clear boundary-line.

The hypohyals in the hyoid arch cannot yet be traced even as prochondrium, whereas the ceratohyals are large and well-developed cylindrical cartilaginous rods. The stylohyals cannot be distinguished in the prochondrial matter which surrounds their extremities, adjoining the hyomandibular. The latter contains a nucleus of cartilage in its frontal edge somewhat below the middleline, but consists otherwise of prochondrium, dorsally changing by degrees into the prochondrial rudiment of the auditory capsule. The frontal edge of the hyomandibular is excavated to make room for the spiracle rudiment. The hyomandibular is pierced by the ramus hyoideomandibularis of the nervus facialis.

In the occipital region the notochord is somewhat recurved ventrally, in the labyrinthal somewhat dorsally, which gives it the faintly S-shaped form characteristic of *Amia*. The tip of the notochord lies closely behind the hypophysis.

*Stage 3.* Total length 8—8.8 millimetres. (Figs. 1 and 2.)

The primordial cranium still agrees in essentials with the conditions in previous stages, although the prochondrium has to a great extent been replaced by cartilage. In the neural cranium the trabeculae (*Tb*) have with exception of their frontal third been transformed into cartilage, which a perichondrium clearly delimits from the mesenchyma.

In the parachordals (*Pch*) the development into cartilage has progressed in a caudal direction. The posterior part, however, from the hind edge of the capsula auditoria, still chiefly consists of prochondrium or a prochondrial mesenchyma. In this rounded cartilage cells are found together with elongated mesenchyma cells. In the vagus region the parachordals only constitute a thin layer on each side of the notochord. It is also easy at this stage to distinguish a narrower frontal part, stretching rostrally from the "Polknorpel"-plate caudally to the posterior margin of the *facialis*-ganglion without becoming attached to the notochord, and a caudal part, that is broader and, in a literal sense, parachordal. Although there is no perichondrium on the parachordals,

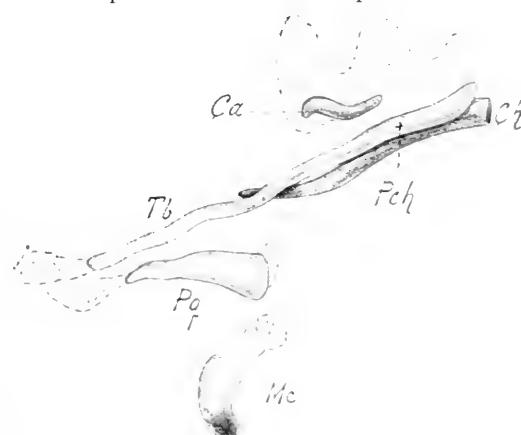


Fig. 1. *Amia calva*. Stage 3. Lateral view of the primordial cranium ( $55 \times 1$ ).

*Ca*, auditory capsule; *NCh*, notochord; *Mc*, Meckelian cartilage; *Pch*, parachordal; *Pq*, palato-quadrate; *Tb*, trabecula. Dotted, prochondrial tissue.

the anterior part is nevertheless clearly delimitated from its environment. The hind part of the latter, especially its inner edge, and the whole caudal part of the same, from the glossopharyngeus ganglion, merges into the mesenchyma without any clear limit. The portion of the parachordals situated between the acousticus and the glossopharyngeus, is continued inward towards the notochord by a thin layer of mesenchyma cells. No occipital cranial rudiment is yet visible.

The rudiment of the labyrinth is ventrally and laterally enveloped by prochondrium, in whose lateral part a cartilage nucleus (*Ca*) has already developed. The connection with the parachordals is, however, still prochondrial.



Fig. 2. *Amia calva*, Stage 3. Ventral view of the primordial cranium ( $55 \times 1$ ).

*Pp*, »Polknorpel»-plate. Other reference letters as in fig. 1.

The state of the visceral cranium is on the whole the same as in previous stages. The pterygo-palatine part of the palato-quadrata (*Pq*), lying towards the roof of the mouth cavity, begins, however, in its caudal part to become more and more detached from its connection with the teeth-rudiments and at the same time to assume the character of prochondrium. This process of detachment as well as that of conversion into cartilage, proceeds in a rostral direction. The caudal parts of the quadrata cartilage are still surrounded by dense prochondrial matter, which is attached to the Meckelian cartilage (*Mc*).

In the hyoid arch the hyomandibular to a great extent becomes changed into cartilage.

#### *Stage 4.* Total length 9,3 millimetres. (Figs. 3 and 4.)

This stage also is characterized by a general differentiation of the elements formed in the earliest stages, without any fundamentally new parts having arisen.

The trabeculae (*Tb*) now are almost entirely transformed into cartilage and surrounded by perichondrium. Only their tips are capped with prochondrial tissue, from which their growth in length is effected. Their frontal parts are dorsoventrally somewhat flattened, but otherwise keep their original cylindrical shape. The rudiment of the future plenum orbitonasale between their front tips could already in the previous stage be distinguished

in the mesenchyma. This rudiment is now developed into a narrow prochondrial bridge hanging together with the prochondrial tips of the trabeculae.

The frontal ends of the parachordals (*Pch*) are somewhat distended, giving the "Polknorpel"-plate the shape of a triangle with the base in front. That part of the parachordals, which lies along the *facialis*-ganglion, is practically unchanged. Immediately behind the *facialis* a change has, however, taken place: a cartilage bridge having developed between the periotal cartilage and the parachordals. In consequence of this a *commissura basicapsularis* (*Can*) has arisen. In relation to the auricular capsule it seems to occupy an unusually rostral situation. It keeps the same position, however, in relation to the ganglia as the first-formed *commissura* in *Lepidosteus* and *Salmo* and is consequently the *commissura anterior*. Behind the *commissura* the parachordals again become broader but assume the same indistinct outlines as before, while at the same time they approach the notochord. They only become definitely attached to the latter behind the *glossopharyngeus* or on a level with the posterior part of the auricular capsule. Between the *glossopharyngeus* and the *vagus* they consist of a tissue, in the middle of which typical young cartilage can be distinguished, while the peripheral parts contain elongated mesenchymatic cells. Behind the *vagus* the parachordals assume the character of a mesenchymatic tissue with somewhat more closely packed nuclei than is the case in the surrounding region. This tissue clothes the lateral surfaces of the notochord, finally disappearing imperceptibly.

In the lateral and basal surfaces of the auricular capsule (*Ca*) intense development into cartilage has begun to take place. Owing to the difficulty of drawing a boundary-line between cartilage and prochondrium the outline of the auricular capsule has an irregular appearance in the reconstruction of fig. 3. Cartilage has also developed in the rostral end. At the same time the region of the labyrinth has increased considerably in a caudal direction. The



Fig. 3. *Amia calva*. Stage 4. Lateral view of the primordial cranium ( $55 \times 1$ ).

*Ca*, auditory capsule; *Ch*, notochord; *Hm*, hyomandibular; *Mc*, Meckelian cartilage; *Pch*, parachordal; *Pq*, palato-quadrate; *Tb*, trabecle. Dotted, prochondrial tissue.

distance between the posterior edge of the auricular capsule and the region of the vagus has in consequence greatly diminished.

In the visceral cranium the development into cartilage also continues. Curiously enough the tip of the palato-quadrate (*Pq*), where the ethmopala-tine joint will form later, has changed into typical young cartilage, while the greater part of the pterygo-palatine part remains in the prochondrial stage and the parts lying closest to the cartilage are still mesenchymatic. The quadrate part has the form of a vertical plate. Close to the Meckelian cartilage (*Mc*), with which it is prochondrially connected, it strongly increases

in both dimensions. Its proximal ends are turned outwards.

The shape and position of the Meckelian cartilage do not differ from what has previously been described. In the hyoid arch an hypohyale below and a stylohyale above may now be distinguished in the prochondrial tissue round the ends of cerato-hyale.

The hyomandibular (*Hm*) is an elongated triangular formation, whose downward tip — processus symplecticus — is separated from the palato-quadrate by indifferent embryonical mesenchyma.

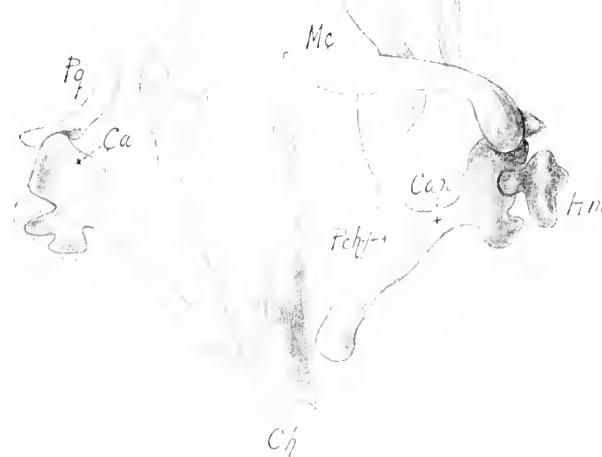


Fig. 4. *Amia calva*. Stage 4. Ventral view of the primordial cranium ( $55 \times 1$ ).

*Can*, commissura basicapsularis anterior. Other reference letters as in fig. 3.

Somewhat above the tip the stylohyale becomes attached to the posterior edge. It is not possible to draw any distinct line in the hyomandibular between the young cartilage and prochondrium. Typical young cartilage, however, exists in the tip of the processus symplecticus. The upper edge at a certain section becomes fused with the peri-otical cartilage, a condition also met with in *Lepidosteus* (VEIT 1911).

The cranium has now passed the first period of its development, during which the neural cranium consists only of trabeculae, parachordals and the peri-otical cartilages. The continued development is based on these rudiments, which thereby lose their independence and enter into other larger complexes. It may therefore now be suitable to compare the earliest development of the

## THE CRANIAL DEVELOPMENT OF TELEOSTOMIAN FISHES

cranium of *Amia* with corresponding stages of the few fishes described by previous authors.

In the *Acanthias* and the *Pristiurus* (SEWERTZOFF 1890) the parachordals are the first skeletal rudiments. They are constructed in the form of undivided cartilage lamels along each side of the frontal part of the notochord, the tip of which they, however, leave free, and can be divided into one occipital, segmented part behind the vagus and one frontal, unsegmented portion. The rudiment of the auricular capsule forms a continuum with the latter already at the prochondrial stage.

In the *Acipenser*, which has also been investigated by SEWERTZOFF (1895), the mesotic and the occipital parts have gained somewhat greater independence. The mesotic part begins to develop somewhat earlier than the occipital. Both become independently converted into cartilage, although soon becoming fused.

In the *Lepidosteus* it is likewise the mesotic part which first begins to develop (VEIT 1911). In VEIT's stage II the cartilaginous parachordal ends already closely behind the trigeminus and at some distance from the notochord. Along the latter a dense mesenchyma lies in the caudal continuation of the parachordals as far as caudal to the vagus trunk. In stage III this posterior part of the parachordals has also become transformed into cartilage. VEIT does not say whether this part has developed from a special cartilage nucleus, although this is probably the case. It is, however, segmented and, partly for this reason, partly because of its position caudad to the vagal nerve, belongs in consequence to the occipital region of the skull.

From STÖHR's description of the development of *Salmo* (1882) and from SWINNERTON's (1902) of *Gasterosteus* it is also evident that the parachordals arise in two independent portions. SWINNERTON does not enter into the details of the earliest development, but STÖHR's description shows that what he calls "die hinteren Parachordalplatten" arise first. In the earliest stage they are bounded in front by the nervus vagus and join the notochord. Somewhat later the trabeculae form independently, and behind them, at some distance from the notochord, the "vorderen Parachordalplatten" originate. These are attached to the posterior plates by means of prochondrium, which meanwhile have grown towards the front and now reach to a point somewhat rostral to the vagus. Still later the posterior parachordal plates stretch so far forward that their frontal part lies between the posterior thirds of the auricular capsules. This frontal part is considerably thicker than the hind part. In the basal plate three regions may consequently be distinguished on each side of the notochord, *viz.* the anterior parachordal plate, the mesotic part of the posterior parachordal plate and the occipital part of the same. The occipital arches originate in this latter part. In a still later stage, the mesotic

region reaches as far as the middle of the sacculus. The hind parts of the anterior parachordals approach the notochord more and more.

In comparing *Salmo* as described by STÖHR and *Gasterosteus* as described by SWINNERTON it seems probable that the occipital part of SWINNERTON corresponds to the posterior (occipital) part of the posterior parachordal plates of STÖHR, while SWINNERTON's mesotic part corresponds to the anterior parachordal plates as well as to the mesotic part of the posterior plates in STÖHR's description. Unfortunately, neither gives a detailed description of the position of the different parts in regard to ganglia and nerve exits. STÖHR, however, states that his posterior parachordals stretch at least as far forward as the middle of the sacculus, in which case they would form a large part of the mesotic section, judging by SWINNERTON's fig. 1.

Those parts of the parachordals in *Amia* whose development I have just described, evidently correspond to the mesotic cartilages of *Acipenser*, to the mesotic part of the parachordals in *Gasterosteus* and the parachordals in *Lepidosteus* which have arisen in VEIT's stage I. The rostral part of the parachordal in *Amia* (which is situated along the *facialis-ganglion*) corresponds in position as well as in form to STÖHR's anterior parachordal plate. The posterior part corresponds to the anterior (mesotic) part of STÖHR's posterior parachordal plates. Of the occipital part there are as yet only mesenchymatic traces in *Amia*. The real parachordals should consequently be: in *Amia* the hitherto cartilaginous parachordal elements, in *Gasterosteus* the mesotic cartilages and in *Salmo* the anterior parachordal plate in addition to the mesotic portion of the posterior parachordal plate. *Salmo* differs from all other described species by the early and isolated appearance of the posterior parts of this parachordal and the early appearance of the occipital region, which immediately becomes connected with the parachordal.

In *Amia* the late development of the posterior (notochordal) parts of the parachordals as well as of the occipital cartilages is remarkable. Even at stage 4 it is only the caudal parts of the parachordals which become attached to the notochord. An unusually large basicranial opening thus is formed, in which a greater part of the notochord extends than is the case in other species. This extraordinary broadening of the cranium, of which there is no indication in the *Selachii*, the cartilaginous *Ganoids*, *Lepidosteus*, the *Teleosts* or in the lung fishes (*Ceratodus*, SEWERTZOFF 1902), must be looked upon as a secondary condition. It also appears in the development of the prechordal parts of the cranium. In reality the trabeculae also lie with their rostral sections comparatively far apart.

SEWERTZOFF has with regard to the ontogenetical origin of the trabeculae and the parachordals distinguished between two types. The first type, to which belong *Selachii*, *Ganoids*, *Teleosts*, *reptiles* and *birds*, is characterized by the separate origin of the trabeculae and the parachordals and by

the fact that the trabeculae are not connected with the notochord. In the other type, comprising Petromyzonts, Anura, Urodela and Dipnoi, the trabeculae together with the parachordals form a parachordal plate. It is, however, impossible to range *Amia* in this scheme, because the first cartilaginous rudiment in the neural cranium is a plate, in which trabeculae (and eventually the "Polknorpel", which cannot here be pointed out as free cartilages) and parachordals meet. The trabeculae, however, are not connected with the notochord.

With regard to the form of the notochord, the well-developed S-shaped curve of its intercranial part (see figs. 1 and 3) should be observed.

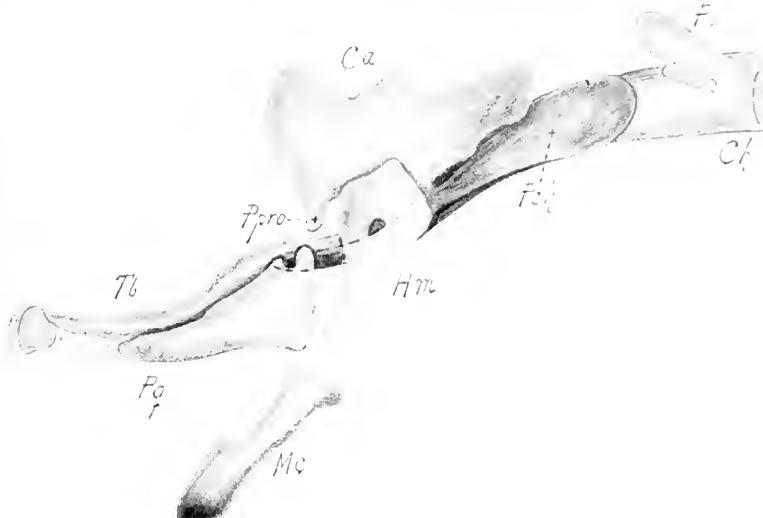


Fig. 5. *Amia calva*. Stage 5. Lateral view of the primordial cranium ( $55\times 1$ ).  
Ca, auditory capsule; Ch, notochord; Hm, hyomandibular; Mc, Meckelian cartilage; Po, notochord; Po, occipital arch; Ppro, prootic process; Pg, palato-quadrate; Tb, trabecle. Dotted, prochondrial tissue.

*Stage 5.* Total length 9.2—9.9 millimetres. (Figs. 5 and 6.)

This stage is chiefly characterized by the origin of a cartilaginous connexion between the trabeculae and by the first appearance of cartilage in the occipital region. Further prochondrium, or mesenchyma, has to a great extent been transformed into cartilage.

Between the trabeculae, whose rostral ends have become yet more flattened, a narrow chondral bridge, commissura trabecularis (*Ct*) has now been formed, a short distance behind their tips. The tips—*cornua trabecularum*—are still covered by prochondrium, which also forms the caudal edge of the cartilaginous bridge itself. The latter is the first rudiment of the *planum orbitonasale*.

Through the arising of the latter a large *fenestra basieranialis* has been formed, in which two sections may be distinguished, one in front, bounded on the side by the diverging trabeculae, and one behind, in the centre of

which lies the notochord and which is bounded laterally by the parachordals. The boundary between these two parts goes through the rather broad plate in which the trabeculae, the "Polknorpel" and the parachordals join and between which the hypophysis is situated. In the angle formed between the trabeculae and the projecting rostral tip of this plate on each side runs the arteria carotis interna. From the lateral part of this plate a process projects caudad and is connected by prochondrium to another process,



Fig. 6. *Amia calva*, Stage 5. Ventral view of the primordial cranium ( $55\times 1$ ).

*Can*, commissura basicapsularis anterior; *Ct*, commissura trabecularis; *Fb*, fenestra basiangularis; *Feb*, fenestra basicapsularis; *Fof*, foramen for facialis. Other reference letters as in fig. 5.

processus prooticus (*Ppro*), from the labyrinthal cartilage. In the angle between the former process and the plate lies the ramus palatinus of the facialis-nerve. The rest of the foramen (*Fof*) which has thus arisen is for the most part filled by the facialis ganglion, from which issues in the caudal part of the opening the truncus hyoideomandibularis. This foramen is bounded caudally by the commissura basicapsularis anterior (*Can*), which has increased in breadth. A commissura posterior can hardly be said to exist, for the auricular cartilage is separated caudally from the parachordals by a narrow

fissure. Almost the whole opening (*Feb*) behind the commissura basicapsularis anterior is filled by the glossopharyngeus ganglion, which lies close to the sacculus. According to VEIT (1911), the conditions in *Lepidosteus* are very much the same: a commissura basicapsularis posterior forming rather late there, which is also the case in *Amia*. The opening situated between the commissura anterior, the parachordals and the auricular cartilages on either side, VEIT calls (l. c. pl. A) fissura basicapsularis. This fissure is of course homologous with the fenestra basicapsularis in other vertebrates. VEIT points out the manner in which it originates in *Lepidosteus* as a remarkable peculiarity. It seems to me, however, that too much importance ought not to be attached to this origin of the fenestra basicapsularis, which is evidently common to *Amia* and *Lepidosteus*. According to SWINNERTON (1902, pl. 28) this fenestra is formed in the stickle-back in the same way as in *Amia* and *Lepidosteus*, and in *Cyclopterus* (UHLMANN 1921) the posterior commissura appears rather late. Thus the early appearance of commissura posterior is not a characteristic feature of the Teleosts generally. On the whole, it is probably difficult to form general opinions on the basis of the insignificant material for comparisons which is to hand, especially as the earlier authors have not taken into consideration the position of the cartilaginous parts especially with regard to the position of the ganglia and of the nerves.

The parachordals, in the posterior part of fenestra basicapsularis first increase considerably in breadth, then become rapidly narrower, and on the level of the exit of the vagus they form a thin cartilaginous covering on each side of the notochord. This cartilaginous covering changes caudally successively into mesenchymatic tissue. Medially the parts of the parachordals lying in front of commissura basicapsularis still lack perichondrium, and send out a thin lamel from their medial side towards the notochord. This lamel is indicated on the transverse sections by a fibrous structure in the mesenchyma. Behind the commissura there is no perichondrium whatever.

The auricular capsule (*Ca*), which has grown so vigorously towards the front that its rostral end is on a level with the tip of the notochord, now consists almost entirely of cartilage, which, however, as yet lies only ventrally and laterally. Only at its rostral end is the labyrinth also dorsally covered with cartilage.

The notochord, which still preserves its S-shaped curve in the sagittal plane, reaches with its tip as far as to the hypophysis, into whose tissues it even penetrates a little way.

In the occipital region cartilage begins to appear at this stage. The parachordals become, as above mentioned, much thinner in the vagus region and then continue caudad in the shape of a thin mesenchymatic stripe, covering the notochord laterally. Then begins a new section of cartilage.

consisting on each side of a thin cartilage plate, which lies on the dorso-lateral side of the notochord. From these cartilage plates the so-called occipital arches (*Po*) project obliquely forward, upward and outward.

These cartilages, first described by ALLIS (1897) and later exhaustively treated by SCHREINER (1902) in connection with the question of the development of the occipital region, correspond altogether in respect of their role in the cranium with those formations of the Teleosts which STÖHR has described as Occipitalpfeiler (Pila occipitalia). The "Occipitalspänge" (SCHREINER) in *Amia* are consequently completely analogous with the Pila occipitalia. Whether they also are homologous with the latter is a question which can only be settled by a study of the metamerism in the occipital region in *Amia* and the Teleosts.

These "Occipitalspänge" are in any case homodynamic or serially homologous in the Ganoids as well as in the Teleosts in much the same way as e. g. the posterior fins, which may develop within different metameres and with the cooperation of a varying number of segments.

Since the question of the number of metameres in the occipital region can hardly be considered as finally settled even within the different groups of Teleosts, and since this does not prevent the cartilage arches in question from being designated throughout as Pila occipitalia, I see no reason to introduce a new name in the case of *Amia*, but consider myself fully justified in using STÖHR's name here also.

In the visceral cranium the Meckelian cartilages begin to deviate from the characteristic transverse position they have occupied in earlier stages and are now directed more frontad, a circumstance depending upon their growth in length. In the palato-quadrate the development into cartilage continues rostrad.

Finally it should be mentioned that the rudiment of the first cranial bones appears, at this stage. From the hypophysis, caudally, to the opticus, rostrally, a cylindrical aggregation of cells extends in the central line between the trabeculae and somewhat ventral to the latter. This aggregation is the osteoblast rudiment, from which the parasphenoid is formed. A similar but considerably shorter aggregation of cells in the posterior parts of the maxillary fold is the first indication of the maxillary.

*Stage 6. Total length 10—11 millimetres. (Figs. 7 and 8.)*

The commissura trabecularis formed in the previous stage has now become expanded into a planum orbitonasale (*Plon*). Rostrally this extends as far as the tips of the trabeculae, which have grown at the same time, till they reach the back part of the nasal sacs. The caudal edge of the planum is situated at the opticus, there forming the frontal boundary of the fenestra basicranialis (*Fb*).

I consider the name "plenum orbitonasale", introduced by VEIT, more appropriate than the names hitherto used, *viz.* "Ethmoidal-plate" (SWINNERTON 1902) "subnasal lamina" (PARKER 1873) and "rostral plate" (McMURRICH 1883). On the one hand, the name introduced by VEIT denotes more clearly the future role of this organ, and on the other the manner of its development agrees more closely with the conditions in the species upon which VEIT has based his description, namely *Lepidosteus*. It is true that in *Salmo* a cartilaginous commissura is also formed between the front tip of the trabeculae (GAUPP and PARKER), but the trabecula communis, formed by the fused trabeculae merges with the posterior edge of the commissure.

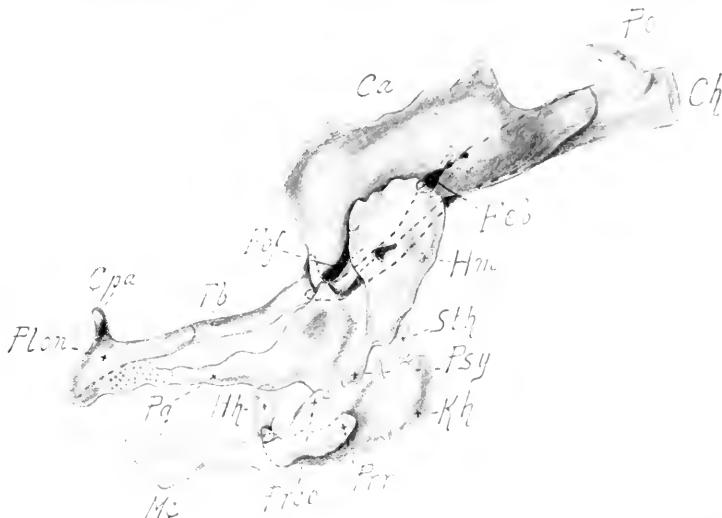


Fig. 7. *Amia calva*. Stage 6. Lateral view of the primordial cranium (43 $\times$  1).

*Ca*, auditory capsule; *Ch*, notochord; *Cpa*, parethmoidal horn; *Fib*, fenestra basicapsularis; *Fof*, foramen for *facialis*; *Hh*, hypohyal; *Hm*, hyomandibular; *Kk*, ceratohyal; *Me*, Meckel's cartilage; *Flon*, orbito nasal plate; *Po*, occipital arch; *Py*, palato-quadrata; *Prc*, processus coronoideus; *Prr*, processus retroarticularis; *Psy*, symplectic process; *Sth*, stylohyal; *Tb*, trabecula. Dotted, prochondrial tissue.

On the front half of the plenum there is on each side and lateral to the brain a short process, directed obliquely upwards and outwards with its inner side lying close to the brain. These two processes are the cornua parethmoidalia (*Cpa*).

The entire length of the parachordals has now become fused with the auricular capsule. The "fissura" basicapsularis of the previous stage has narrowed to a fenestra basicapsularis (*Fib*) of comparatively small dimensions. A fenestral formation of the same size has arisen on a level with the rostral parts of the auricular capsule, the previous prochondrial connection having now been converted into cartilage. This foramen (*Fof*) encloses in its rostro-medial part the ramus palatinus of the *facialis* nerve. In its caudal angle runs the *truncus hyoideomandibularis*, the space between the

nerves being occupied by the *facialis* ganglion. According to SWINNERTON the opening for the *facialis* in *Gasterosteus* is formed in much the same manner. At this point a processus prooticus forms which finally reaches the parachordals, with which it becomes fused. A similar prootic process (Figs. 5, 6, *Ppro*) can also be traced in *Amia*.

The parachordals having become fused with the notochord — approximately on a level with the *fenestra basicapsularis* — they run, lateral to the notochord in the form of a pair of plates of the same breadth as the notochord. Behind the *commissura posterior* (*Cpo*) they grow narrower rather rapidly and are then transformed, as in the previous stage, into a covering of compact mesenchymatic tissue on the sides of the notochord, this tissue showing crescent-shaped on the cross sections.

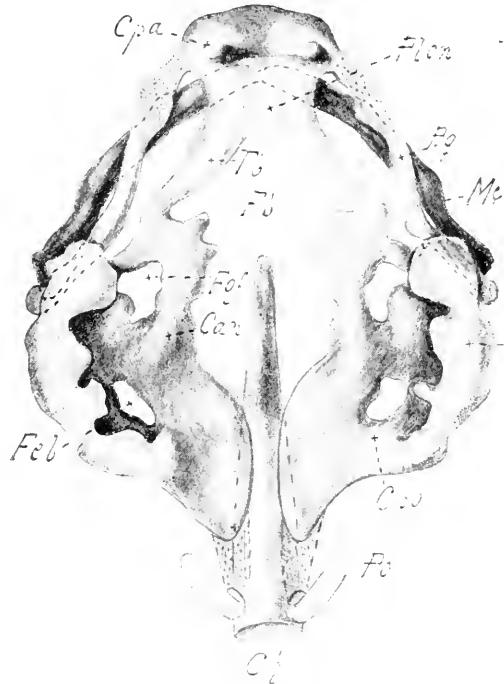


Fig. 8. *Amia calva*, Stage 6. Dorsal view of the primordial crane ( $43 \times 1$ ).

*Can*, commissura basicapsularis anterior; *Cpo*, commissura basicapsularis posterior; *Fb*, fenestra basicranialis. Other letters as in fig. 7.

this region has apparently proximated to the expansion of the labyrinthal region.

The notochord now enters between the infundibulum and the hypophysis. Traces of beginning degeneration may be observed in this part of the notochord, a fact that is all the more remarkable as no such thing has been noticed either by VEIT during the embryonal development of *Lepidosteus* or by SWINNERTON in *Gasterosteus*, whereas in *Polypterus* considerable retrogression of the notochord may be observed.

In the visceral cranium the prochondrial connections between the diffe-

rent cartilaginous elements still exist, and the palatine part of the palatoquadratus has not yet become converted into cartilage.

The Meckelian cartilage has increased considerably in length and now almost occupies the normal position of the future lower jaw. A processus retroarticularis may clearly be traced in the proximal part, and the rudiment of the processus coronoideus may also be observed.

The cartilaginous connection between the hyomandibular and the auricular capsule has been replaced by a tissue of a more mesenchymatic nature. On the hyomandibular a well-marked processus symplecticus (*Ps*) may now be observed.

In addition to the previously developed osteoblastic rudiments of the parapophenoid and the maxillaries, similar rudiments for the vomera now appear, in the shape of paired, elongated masses of cells below the margins of the planum orbitonasale, in front of the rudiment of the parapophenoid. In the latter a thin lamel of bone is already visible.

*Stage 7.* Total length 10.6 millimetres. (Fig. 9.)

The planum orbitonasale (*Plon*) has only slightly increased in extent. Its front edge still lies near the posterior part of the nasal sacs. In front of it not only the lobi olfactorii but also part of the rest of the telencephalon are situated. Above the front edge of the planum or approximately on a level with the anterior margin of the eyes lies the paraphysis

The processes already developed on the orbitonasal plate in the previous stage and which I have designed cornua parethmoidalia (*Cpa*) now have assumed a more crestlike appearance in their basal parts on account of their extension in a caudal direction. Rostrally they have greatly lengthened in



Fig. 9. *Amia calva*. Stage 7. Dorsal view of the primordial crane (43×1).

*Ca*, auditory capsule; *Ch*, notochord; *Cpa*, parethmoidal horn; *Csu*, supraorbital cartilage; *Fb*, fenestra basicranialis; *Fe1*, foramen for gangl. glossophar.; *Fe2*, foramen for nerv. palat. fac.; *Fof1*, foramen for nerv. palat. fac.; *Fof2*, foramen for truncus hyoideomandibularis; *Plon*, planum orbito nasale; *Po*, pila occipitalia; *Pq*, palatoquadratus; *Rpa*, parethmoidal ridge; *Tb*, trabecula.

a dorsal direction, approximately on the level of the front part of the pulvinar. Each process is distally flattened into a thin, small plate, lying close to the telencephalon dorso-laterally. Somewhat behind these cartilage plates, between the eye and the mesencephalon and on a level with the posterior edge of the commissura posterior, lie a pair of elongated, roughly threesided pieces of cartilage, *cartilagine supraorbitales* (*Csu*). Together with the cornua *parethmoidalia* they constitute the first rudiment of the supraorbital cartilage bridge. They are connected with the cornua by a stripe of mesenchymatic tissue. There is on the other hand no trace of any connection with the auricular capsule.

The *planum orbitonasale* has increased considerably in length. At the same time the whole cranium has increased in breadth, which may be seen from the position of the free caudal parts of the *trabeculae*, which diverge more and more. The rostral part of *fenestra basicranialis* becomes hereby considerably diminished.

In the parachordal part of the cranium a beginning division of the two fenestral formations may be observed. In the front opening, *fenestra anterior*, a transverse bridge is formed dividing the fenestra into a frontal opening (*Fof 1*) through which only the *nervus palatinus* of the *facialis* passes, and a posterior opening (*Fof 2*) which is filled to a great extent by the *facialis* ganglion now fused with the *trigenimus-ganglion*. In a similar way, the *fenestra posterior* (s. *basicapsularis*) is divided by a prochondrial bridge into two foramina, one frontal (*Feb 1*), which is filled by the *glossopharyngeal* ganglion, and one posterior (*Feb 2*), through which the *nervus glossopharyngeus* issues to bend forward later and become fused with its ganglion. The parachordals are as yet only in mesenchymatic connection with the occipital region.

The degeneration of the notochord has proceeded farther caudad.

In the occipital region cartilage is still found only in the two *pila occipitalia*.

Ossification now appears also in the vomeral and the maxillar rudiments, besides which *dentale* and *prespleniale* have been formed on the Meckelian cartilage.

*Stage 8.* Total length 12 millimetres. (Cfr figs. 9, 10, 11.)

The orbito-nasal plate stretches as far forward as the tip of the *lobi olfactorii*, on a level with the frontal edge of the posterior nasal openings, and has increased in breadth, especially as regards its frontal part. About midway, between the two *nervi olfactorii*, rises a short, clumsy median process, the rudiment of the *septum nasi*. Caudally *septum nasi* becomes broader and lower and then runs caudad on each side to merge into the *cornua parethmoidalia*. The orbito-nasal plate has expanded laterally in this section. Each of the

## THE CRANIAL DEVELOPMENT OF TELEOSTOMIAN FISHES

parethmoidal ridges has thus been apparently transported in a more medial direction. It is at this spot that the anterior eye-muscle canals arise in the following manner: from the margin of the orbito-nasal plate and at right angles to it a pair of longitudinal cartilaginous processes form, which merge into the parethmoidal ridges. A short canal, open at both ends, is hereby formed between the processes, the ridges and the dorsal side of the orbito-nasal plate. The *Mm. obliqui inferiores* and *superiores* find their basal attachment in the canals.

Farther caudad, approximately on a level with the frontal edge of the pulvinar, the planum orbito-nasale decreases at the same time considerably in breadth.

At this stage the framing of the orbit has been completed. The parethmoidal horns have increased in breadth and extend in curve, first dorsal, then caudad, to merge finally into the supraorbital cartilages, between the telencephalon and the diencephalon. The supraorbital cartilages have on the other hand lengthened caudad and united with the rostral end of the auricular capsule. The different elements of the *taenia marginalis* which has thus arisen may however still be clearly distinguished. The parethmoidal horns are thin cartilaginous lamels, which in the cross sections are approximately concavo-convex, with the convexity laterad. The supraorbital cartilages still retain their three-sided, blunt-edged form. A suture is plainly visible at their junction to the auricular capsule.

The parethmoidal elements of the orbital arch are connected above the pulvinar by a thin membrane. Above the posterior part of the epiphysis and on each side of the latter a thin and narrow piece of cartilage may be distinguished. The cartilage is prochondrially connected with the lateral cartilaginous parts. These paired cartilages are the epiphyseal cartilages. The parachordals are now connected with the occipital region by means of cartilage.

From the rostral end of the auricular capsule a blunt, latero-rostrally directed process juts out. Its posterior part is pierced by a foramen, through which runs the ramus oticus of the facial nerve to a sense-organ situated in the sensory canal in the angle between the process and the auditory capsule, and to the sense-organ in the spiracular recess. This process cannot be anything else than VEIT's *processus postorbitalis* in *Lepidosteus*, though I cannot consider this name very suitable. The term *processus postorbitalis* is generally understood to denote that process in the Teleosts which juts out rostrally from the labyrinthic capsule, unites later with the epiphyseal cartilage, forms the *taenia marginalis posterior* (SWINNERTON, 1882; UHLMANN, 1921), and is consequently the process, which according to VEIT's pictures, completely corresponds to his *cartilago supraorbitalis*. In my opinion, the process in question may be regarded as the frontal part of the *crista parotica*, which develops later, and might thus suitably be termed *processus paroticus*.

Immediately behind this the cartilaginous environment of the spiracular canal originates in the shape of a narrow cartilage bridge, projecting from the auricular capsule, its rostral end approaching the caudal part of the processus paroticus, with which it merges at the next stage.

To the ossifications mentioned at the previous stage have now been added the premaxillaries. The circum-orbital bones of the sensory canal have now also begun to appear.

*Stage 9.* Total length 13.6—14 millimetres. (Figs. 10 and 11.)

The most important changes in the primordial cranium have occurred in the ethmoidal and the orbito-temporal region.

The orbito-nasal plane has very much the same rostral extension as at the previous stage. In its tip, a short median process has formed, which is the



Fig. 10. *Amia calva*. Stage 9. Lateral view of the primordial crane ( $25 \times 1$ ).

*Aem*, anterior eye-muscle canal; *Csp*, spiracular canal; *Epb*, epipharyngeal bar; *Fgb*, foramen for ganglion glossopharyngeal; *Fhm*, foramen through the hyomandibular for. n. hyoideomandib.; *Fof1*, foramen for truncus hyoideomandib.; *Hh*, hypohyal; *Hm*, hyomandibular; *Kh*, ceratohyal; *Mc*, Meckel's cartilage; *Po*, occipital arch; *Ppar*, parotic process; *Ppb*, parapharyngeal bar; *Pq*, palatoquadrate; *Pro*, coronoid process; *Prr*, retroarticular process; *Pyr*, symplectic process; *R*, rostrum; *Rpa*, parethmoidal ridge; *Sh*, stylohyal; *Sn*, nasal septum.

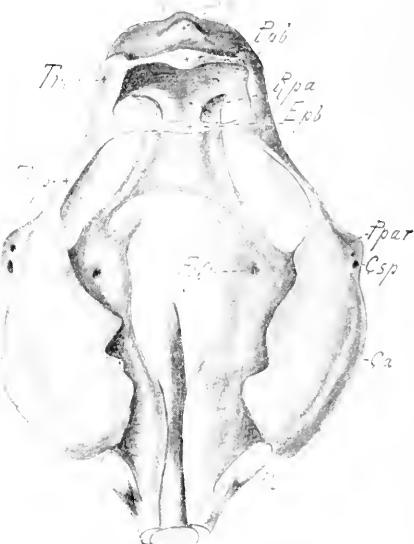


Fig. 11. *Amia calva*. Stage 9. Dorsal view of the primordial crane ( $25 \times 1$ ). *Fof1*, foramen for nerv. palat. fac.; *Tma* and *Tmp*, *Tenia marginalis* anterior and posterior. Other letters as in fig. 10.

rudiment of the rostrum (*R*). Septum nasi (*Sn*) has lengthened and lies now with its tip in front of the olfactory nerve; its pre-olfactory, dorsally flattened part lies closely under the lobi. Behind the nasal saes, from whose caudal part the olfactory nerves emanate, the septum is flattened, as at the previous stage, and runs out caudally in two slightly diverging longitudinal ridges, which in the manner described above, join the parethmoidal ridges and take part in the formation of the frontal eye-muscle canals. The parethmoidal horns unite over the frontal part of the paraphysis in a narrow bridge, the parapharyngeal bar (*Ppb*).

Above the posterior part of the epiphysis a unified cartilaginous band, the epiphyseal bar (*Epb*), has now formed, the median part of which has expanded into a small plate. In the lower edge of the *taenia marginalis*, below the epiphyseal bar, a foramen has formed, through which a blood-vessel passes. Immediately behind this foramen lies the point of junction for the supraorbital cartilages and the processes from the pterygoid horns. Caudally the orbito-nasal plate has also lengthened, whereby its posterior edge has become straight instead of curving rostrally inward as before, and the free part of the trabecula has become further reduced. The parachordal part of the *fenestra basicranialis* has consequently also become reduced.

The parachordal plates have not appreciably increased in breadth. The interlabyrinthine part of the *fenestra basicranialis* has on the other hand, become, not only absolutely but also relatively, somewhat broader than before. In its anterior part is situated the hypophysis, somewhat caudal to which lies the notochord, whose tip still shows signs of regression. On each side of the frontal part of the parachordal plate, in addition to the foramen of the *nervus palatinus*, another foramen may be found, situated caudo-laterally to the latter, through which passes the *vena jugularis*, this foramen lying close to that of the *facialis*. This foramen (*Fof 2*) no longer opens ventro-laterally but fully laterad, in consequence of its lateral edge, i. e. the margin of the labyrinthine cartilage, with which the parachordal has never been fused, having now increased in a median direction over the *facialis* ganglion. This cartilaginous section constitutes in fact the posterior part of the roof of the trigemino-facialis chamber.

Dorsally the labyrinth has also become covered with cartilage. Inwards, however, the labyrinth is still open, with the exception of its rostral and caudal ends. Under the frontal part of the labyrinthine cartilage lies the trigeminus portion of the trigemino-facialis complex. It continues caudad as far as the foramen described above (*Fof 2*), in whose posterior part the *truncus hyoideomandibularis* emanates. The whole of this part constitutes the rudiment of the trigemino-facialis chamber, delimited inwards from the brain by the *dura mater*. Dorsally, the trigemino-facialis chamber is thus covered by the floor of the auricular capsule, ventrally by the lateral parts of the parachordals. The rostral and caudal parts of the chamber are open outwards, while the central part is laterally bounded by the prefacial basicranial commissura.

Through the caudal growth of the cranium, the occipital region now appears to have moved farther rostrad. The *pila occipitalia* (*Po*) extend rostrally as far as the caudal end of the labyrinthine cartilage, which they touch, without in any way becoming connected with it. Consequently the *vagus* now passes through a fissura, which is open dorsally, is rostrally bounded by the labyrinthine cartilage, caudally by the *pila occipitalia*, and ventro-medially by the parachordals. In the occipital region, the cartilaginous

covering of the notochord is still limited to a band on its dorso-lateral part. The notochord is nowhere wholly surrounded by cartilage.

In the visceral cranium, the large processus coronoideus (*Prco*), so characteristic of *Amia*, has formed on the Meckelian cartilage, in addition to the caudally-directed processus retroarticularis (*Prr*).

The palato-quadrate (*Pq*), which at stage 7 was rostrally in direct cartilaginous connection with the ethmoidal region, is now separated from the neural cranium by a distinct boundary-plane, and wholly converted into cartilage. Near its caudal end a dorsal process — the metapterygoid process — may be seen indicated on the quadrate part.

On the hyomandibular the narrow processus symplecticus (*Psy*) may be distinguished, its distal part, which is bent over rostrally, approaching continually closer to the joint of the quadrate. The stylohyale (*Sh*) leads towards a ventral process at the upper part of the processus symplectiformis. On the caudal edge of the hyomandibular a well-defined, caudally-directed process has formed, to which the operculum later accedes.

The formation of the greater number of the dermal bones has now commenced. The parietale, supramaxillare and the opercular plates, however, are still lacking. Neither are any chondral bones as yet to be found.

The latest described stages are, in regard to the neural cranium, characterized by the commencing differentiation of the ethmoidal region, by the beginning formation of the orbital frame, and in connection with the latter, by the development of the roof of the cranium and by the approximation of the occipital region to the cranium proper. At the same time the trabecular part of the fenestra basiscranialis has become still more closed, the fusion between the parachordal plates and the labyrinthal cartilages has become more complete in consequence of the foramina between these cartilages having become partly closed, partly divided up into smaller foramina. The reduction of the tip of the notochord has also begun. On the other hand, no further closing up of the parachordal part of the fenestra basiscranialis has taken place.

In regard to the framing of the orbit, this is in *Amia* effectuated from two sources, as is evident from what has already been stated, viz. from the parethmoidal horns and from the supraorbital cartilages. The former increase in size, first dorsally, then caudally, to fuse with the latter, which also increase dorsally and unite with the rostral ends of the labyrinthal cartilages. As the origin of the epi- and paraphysear bars is intimately related to the supraorbital connection, it may be suitable to treat these questions simultaneously.

Verh rather summarily describes in *Lepidostomus* the origin of the supraorbital arch (*taenia marginalis*), the epiphyseal and the paraphysear bars. According to him, a pair of supraorbital cartilages first arise, one on either

side, starting from the rostral end of the auricular capsule. It does not appear whether these cartilages develope independently; they increase, however, in size frontad and somewhat inwards, then unite above the epiphysis to form the epiphysear bar, after which they continue frontad and unite with the paraphysear bar, which is formed of cartilage plates jutting upwards from the ethmoidal region.

SWINNERTON gives a more detailed description of *Gasterosteus*, and UHLMANN of *Cyclopterus*. According to the latter, a pair of independent epiphysear plates arise in *Cyclopterus lumpus* at the 4—5 mm. stage, which fuse medially and thus form the epiphysear bar, rostrally joining the parethmoidal horns, which become fused above the brain. The connection between the ends of the epiphysear bar and the parethmoidal horns is called *taenia marginalis anterior*. Simultaneously with the epiphysear plates, a rostrally-directed post-orbital process develops from the auricular capsule, and unites with the caudally-directed lateral processes from the epiphysear bar to *taeniae marginales posteriores*.

The development proceeds on much the same lines in the stickleback, in which however the posterior *taeniae* never form, a circumstance connected with the reduction of cartilage in the orbito-temporal region during the later stages of embryonic development.

According to SEWERTZOFF and VAN WIJHE, the well-known alisphenoid cartilages (GAUPP's spheno-lateral cartilages), develope in Selachians as independent pieces of cartilage, from which the supraorbital region chiefly develope. The alisphenoid cartilages, which fuse caudally with the rostral end of the parachordal plate, fuse later with the labyrinthal cartilages as well. Between the latter, the parachordal plate and the alisphenoid cartilage a foramen consequently forms, through which the trigeminus and facial nerves pass. VAN WIJHE declares (1904) that in *Acanthias* and *Raja* he has likewise observed independent supraorbital cartilages, which fuse caudally and ventrally with the alisphenoid cartilages, — which he terms *lamina antotica* — and rostrally with the orbito-nasal plate (*lamina antotica*). VAN WIJHE's statements are, unfortunately, very summary, and he has no illustrations to elucidate them. It seems remarkable that these supraorbital cartilages should have escaped SEWERTZOFF's notice when he investigated *Acanthias*. They may possibly be a delicately outlined part, connected by means of prochondrium with the rostral ends of the alisphenoid plates. The "Polknorpel" discovered by VAN WIJHE between the parachordal plate and the trabeculae in the same material, may be explained in the same way. SEWERTZOFF points out that the alisphenoid cartilages by no means only occur in Selachians; he considers that homologous formations are likewise to be found in other group of fishes, as in *Urodeles* and *Lacertilia*, in the shape of pieces of cartilage in the pre-chordal region. These formations always occupy the same position, viz. lateral

to the brain and between the latter and the ocular saccules, dorsal to opticus and rostral to parachordalia and the auricular capsule. SEWERTZOFF has drawn attention to such a piece of cartilage in *Carassius*, frontally rod-shaped, caudally flattened, and connected with the auricular capsule.

UHLMANN considers that the binary epiphyseal plates in *Cyclopterus lumpus* are homologous with the alisphenoid plates, with which, according to him, their position and form correspond.

The conditions in *Amia* are as follows: in the region mentioned by SEWERTZOFF, independent pieces of cartilage, supraorbital cartilages, form, fusing caudad with the auricular capsule in exactly the same manner as the alisphenoid plates. The ventral connection with the parachordals is on the other hand lacking. The supraorbital cartilages are undoubtedly homologous with the alisphenoid cartilages, at all events with the dorsal parts of the latter.

The epiphyseal plates are homologous in *Amia* and the Teleosts. It appears however incredible, that they should likewise be homologous, as UHLMANN suggests, with the alisphenoid cartilages proper, especially as they become primarily connected with the ethmoidal horns, i. e. with rostral elements. They might possibly be homologous with VAN WIJHE's supraorbital cartilages, with which they agree both in regard to position and connection with their surroundings.

Typical for the Teleosts (and *Lepidosteus*?) is the circumstance that, as above-mentioned, in the cases where *taenia marginalis posterior* is found (*Salmo*, *Cyclopterus*), it is chiefly formed of *proc. postorbitales* from the auricular cartilages, while in *Amia* it is formed mainly of the supraorbital cartilages. As, according to the literature on the subject, the *proc. postorbitalis* arises from the auricular capsule, while the supraorbital cartilages form independently, it can hardly be proved that these formations are homologous, as SEWERTZOFF has stated, even if a certain degree of probability makes it conceivable. In any case the *taenia marginalis posterior* forms in *Amia* in a more primitive manner than in the Teleosts (and *Lepidosteus*?), reminiscent rather of the conditions in the Selachians.

*Stage 10.* Total length 19,5 mm. (Figs. 12 and 13.)

In the ethmoidal region a somewhat more sharply defined rostrum may be observed, on the median part of which rises the well-developed *septum nasi*. A comparison with the previous stage shows that the rostral part of the latter has considerably increased in height forming thus a dorsal process (fig. 12, *Sn*). Immediately in front of the tip of *lobi olfactorii*, the *septum nasi* merges caudally as before into a pair of diverging longitudinal ridges, which behind *nervi olfactorii* fuse with the ethmoidal horns. The eye-muscle canals (*Aem*) still open frontad, viz. immediately caudally to the olfactory nerves in the grooves on either side of the *septum*, where the nerves run and whose direct continuation caudad are the eye-muscle canals.

The frontal fontanel situated between the paraphyseal and the epiphyseal bars, which was open at the previous stage, has now closed, with the exception of a spot above the epiphysis, where a foramen remains (*Fore*). Rostrally, the roof of the cranium stretches to the rostral end of the lobi olfactorii, above which it juts out somewhat. Caudally it extends somewhat behind the boundary between the telencephalon and the diencephalon. A short *taenia medialis posterior* (*Tm*) projects from its posterior edge. The foramen above the epiphysis lies immediately in front of the epiphyseal bar, which existed already at the previous stage. Rostrad, the *cavum cerebri* is entirely open.

The most remarkable change noticeable in the labyrinthal region is the rapid development into cartilage of the dorsal parts of the auricular capsule



Fig. 12. *Amia calva*. Stage 10. Lateral view of the primordial crane (25 $\times$ 1).  
*Aem*, anterior eye muscle canal; *Csp*, spiracular canal; *Crpe*, crista parethmoidalis; *Fef<sub>2</sub>*, foramen for truncus hyoideomandibularis; *Hm*, hyomandibular; *Mc*, Meckelian cartilage; *Po*, occipital arch with aliform process; *Pn*, retroarticular process; *Pg*, palato-quadratae; *Prp*, pedicle process; *Prm*, metapterygoid process; *Py*, symplectic process; *R*, rostrum; *Sn*, nasal septum.

(*Ca*). The two laminae have, however, not yet fused in the middle line to form a *tectum synoticum*.

In the occipital region it may be observed that the occipital arches have on either side fused with the posterior end of the auricular capsule. Moreover, from each pilum a triangular flat dorso-medially directed process has formed (*Po*), under which the vagus passes.

At this stage the appearance of the operculum completes the total number of the dermal bones which have now arisen.

*Stage 11.* Total length 21.5 mm. (Cfr figs. 12 and 13.)

In the ethmoidal region a remarkable change has taken place; the well-developed dorsal process on the septum nasi, mentioned in the previous stage,

being now almost completely reduced, simultaneously with the degeneration of a large part of the basal portions of the septum nasi.

The fontanel in front of the epiphyseal bar having closed earlier, the posterior opening has now also begun to close. The formation of new cartilage does not, however, take place from the *taenia medialis posterior*, which has now completely disappeared, but from the edges of the *taeniae marginales*

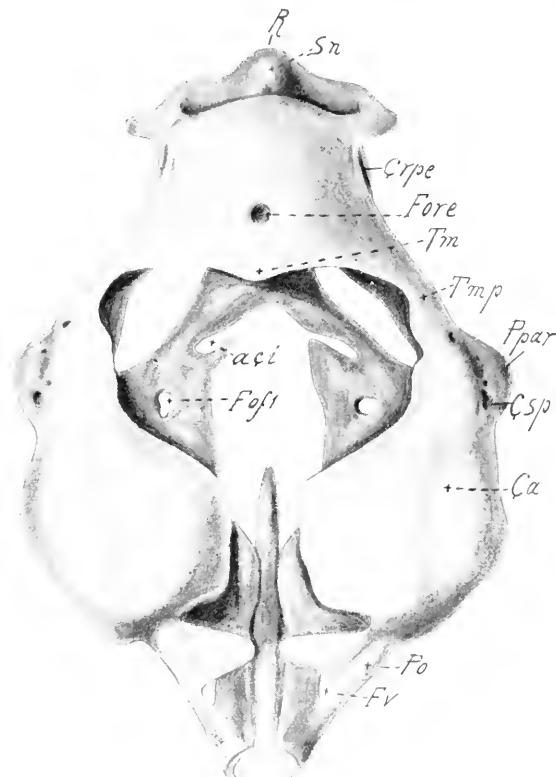


Fig. 13. *Amia calva*. Stage 10. Dorsal view of the primordial crane ( $25 \times 1$ ).

*aci*, incisure for arteria carotis interna; *Fof1*, foramen for *n. palat. fac.*; *Fore*, foramen epiphyseos; *Tm*, *taenia medialis*; *Tmp*, *taenia marginalis posterior*. Other reference letters as in fig. 12.

the brain, approximately over the posterior portion of the trigeminus chamber, where the *truncus hyoideomandibularis* issues from it. This cartilage bridge is, however, still quite narrow, but continues caudad in a broad median process, which runs out caudad in two short lateral tips. These lie approximately on a level with the exit of the *acusticus*.

It is worthy of notice that in *Amia* the posterior portion of the *tectum crani* develops from two points, partly as a real *tectum synoticum*, partly as a *tectum occipitale*, which are divided by a large foramen. In the Teleosts

(*Tmp*). Contrary to what is the case in the Teleosts as well as in *Lepidosteus*, where the posterior fontanel is divided by the well-developed *taenia medialis posterior* into a right and a left section, this fontanel remains undivided in this direction.

The roof of the cerebral capsule is, however, not formed from the orbital region alone, a vigorous development of cartilage having taken place in two more spots, viz. in the occipital region and in the region of the labyrinth. In the occipital region the previously mentioned aliform processes from the *pila occipitalia* have united, forming a cartilage bridge, below which lies the exit of the *vagus*. The *tectum synoticum proper* lies more rostrally and has arisen through the dorsal lamellæ of the auricular cartilages having fused in the middle line above

the tectum synoticum is formed in the shape of a single cartilage bridge, containing the two elements which remain separate in *Amia*. The isolated appearance of these latter, is of course to be explained by the relative independence which the occipital part still enjoys in *Amia*.

Some remarkable changes have also taken place at the base of the cranium. The tips of the medially and rostrally directed processes, which from the frontal part of the parachordals project into *fenestra basicranialis* between the pars trabecularis and the pars interparachordalis of the latter, have now united with the trabeculae. Thus the incisure for the *arteria carotis interna* (fig. 13, *aci*), existing from the earliest stages, has become transformed into a foramen. Only an insignificant portion of the pars trabecularis remains, which is filled by the hypothalamus. The latter is covered from beneath by the parasphenoid, as is also the case with the whole of the *fenestra*. The foramen hypophyseos proper consequently lies in the rostral part of the pars interparachordalis.

The tip of the notochord lies under the oblongate and proves to be still in process of regression. The caudal part of the *fenestra basicranialis*, on the other hand, has not closed to any appreciable extent. The parachordals are still fused with the notochord approximately on a level with the foramen *glossopharyngei*. Only the *nervus glossopharyngeus* traverses the latter. The cranium has closed above the ganglion.

In the ethmoidal region already at stage 10 the beginning of a horizontal cartilage ridge (figs. 12 and 13, *Crpe*) might be observed on the frontal part of the rudiment of the cerebral capsule. The latter has now developed still further in a caudal direction. I have called it *crista parethmoidalis* in analogy with the *crista parotica*, which arises in the same way in the labyrinthal region above the articular socket of the *hyomandibulare*.

*Stages 12 (31.5—34.5 mm.) and 13 (36 mm.). Fig. 14.*

It is only at these stages that the cranium in the ethmoidal region begins to assume an appearance recalling the conditions in the full-grown cranium. This fact is connected with the circumstance that the cranium only now begins appreciably to exceed the brain in length. As is evident from the earlier descriptions, the brain has long been extended in front of the *orbito-nasal* plates.

It was not before stage 9 that the frontal edge of the *planum* lay on a level with the tips of the *lobi olfactorii*. The greater portion of the *nasal sacculus* have therefore lain in front of the *orbito-nasal* plate, which can thus hardly be said to have had a *nasal* region.

Longitudinal growth has been especially vigorous in the rostral parts of the cranium. In front of *cavum cerebri* the cranium consists of the three-cornered ethmoidal plate, which is prolonged frontally into a small *rostrum*

(*R*). On either side of the plate lie the elongated articular surfaces of the palato-quadratae. Immediately behind the articular surfaces the ethmoidal plate becomes rapidly narrower and passes into the planum orbito-nasale proper.

Along the median line of the ethmoidal plate rises a rather low internasal septum (*Sn*), which is thinnest in the centre and somewhat thicker frontad and caudad, merging caudad into cavum cerebri, of which it appears consequently to be a rostral elongation. This internasal septum is, at least for the most part, a new formation, for, as was evident from the conditions in

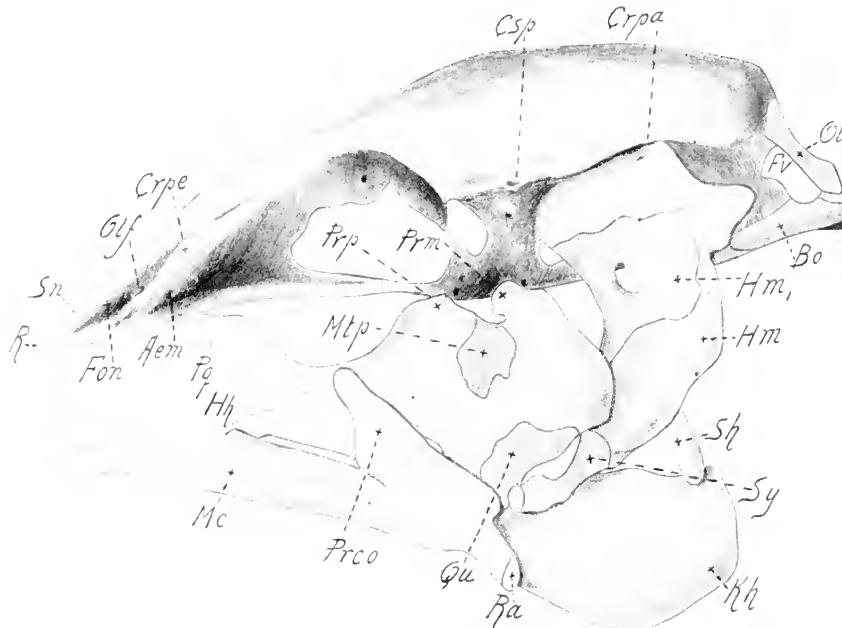


Fig. 14. *Amia calva*. Stage 12. Lateral view of the primordial crane ( $10 \times 1$ ).

*Aem*, anterior eye muscle canal (posterior opening); *Bo*, basioccipital; *Crpa*, crista parotica; *Crpe*, crista parethmoidalis; *Csp*, spiral canal; *Fon*, fossa nasalis; *Fv*, foramen vagi; *Hh*, hypohyal; *Hm*, hyomandibular; *Hm<sub>1</sub>*, hyomandibular bone; *Kh*, ceratohyal; *Mc*, Meekelian cartilage; *Mtp*, metapterygoid; *Ol*, occipitale laterale; *Olf*, foramen olf.; *Pq*, palato-quadratae; *Prco*, coronoid process; *Prm*, metapterygoid process; *Pp*, pedicle process; *Qu*, quadrate bone; *R*, rostrum; *Ra*, retroarticular; *Sh*, stylohyal; *Sn*, nasal septum; *Sy*, symplectic bone.

Amia of 21.5 mm. length, the shorter but higher septum formation, which developed earlier, has degenerated. Unfortunately it cannot be determined on the basis of my material, how this new septum has arisen, since the necessary stages are lacking.

On either side of the septum, the ethmoidal plate forms a shallow completely open depression, the fossa nasalis (*Fon*), bounded medially by the septum nasale, ventrally by the ethmoidal plate, and caudally by the laterally-spreading aliform cristæ parethmoidales (*Crpe*). The latter slope down towards the ethmoidal plate uniting with it at its caudal edge. It is

thus the rostral surface of the *cristae parethmoidales* which forms the *planum antorbitale* in *Amia*.

Thus no really new formations with the exception of the nasal septum have arisen at this stage. The *tectum crani* had at the previous stage its rostral limit close to the tip of the *lobi olfactorii*, with a wide-mouthed opening towards the ethmoidal plate. Its rostral end has now greatly increased. The *nervi olfactorii* now run some distance inside the *cavum* before fusing with the *lobi*. The eye muscle canals occupy the same position as before, although owing to the growth of the ethmoidal parts of the cranium, they now lie laterally and somewhat ventrally to the *cavum*. *Foramen olfactorium (ad-vehens)* is situated in the frontal end of these canals (*Olf*). This foramen lies medially in the *fossa nasalis*, close to the *internasal septum*. The *nervi olfactorii*, having left the *fossa nasalis*, pass through the anterior part of the canals, emerging from them laterally to continue into the *cavum*. The canals open laterally in the orbit in the angle between *planum antorbitale* (s. *crista parethmoidalis*) and *planum orbitonasale (Aem)*.

The *crista parethmoidalis* narrows considerably behind the ethmoidal region, but can be followed in the shape of a low ridge above the orbit. Behind the orbit it again grows broader and passes into the *crista parotica*. *Ramus ophthalmicus facialis*, which innervates the canal organs in the supraorbital sensory canal (ALLIS 1889), runs ventral to the *crista parotica*, but at the junction between the two *cristae* it turns off somewhat dorsally and lies on the dorsal side of the *crista parethmoidalis (Crpa)* in the groove between the latter and the *tectum*. It retains the same position in the ethmoidal region consequently taking a downward course over the *planum antorbitale* instead of piercing it.

The cartilage bridges previously found dorsal to the brain have now united forming a single roof over the entire brain cavity. The *foramen* of the *epiphysis* has now likewise closed.

During the latest stages, the *visceral cranium* also exhibits a powerful longitudinal growth.

In the Meckelian cartilage this longitudinal growth has taken place most rapidly in the posterior half. The *processus coronoideus (Prco)*, of which a rudiment was already indicated at earlier stages, has gradually developed into a fair-sized formation. I have not been able to corroborate VAN WIJHE'S (1881) statement that the *processus coronoideus* is furnished with a large piece of cartilage, connected with the Meckelian cartilage, as he assumes developing independently.

The *palato-quadrate (Pq)* has greatly increased in length, especially the central portion. The *quadrate* part, which as late as stage 9 retains the form of a triangle, which narrows rostrally rather slowly, merging in the *pterygo-palatine* part, assumes at later stages a more *quadrate* form. One

corner is directed frontad and merges in the pterygo-palatine part. The quadrate joint is situated in the ventrally directed corner, the opposite corner being the processus metapterygoideus (*Prm*). Rostral to the latter lies a somewhat shorter process, divided from the former by an incisure, in the bottom of which the first rudiment of the metapterygoid appears. The more rostral of the two processes is the "pediculus process" (*Prp*), already pointed out by SWINNERTON, in certain Teleosts, as well as in some of the lower fishes. The pedicle process might possibly be the more rostral of the two processes already existing in stage 4 on the rudiment of the as yet threecornered palatoquadrate (fig. 3). This process is almost completely obliterated in the intervening stages, consequently reappearing rather late. According to SWINNERTON, this process might indicate the existence of an ancestral pedicular articulation, existing simultaneously or even previously to the ethmo-palatine articulation. "The fact that in *Petromyzon* the facial skeleton commences as an outgrowth — the pedicle — from the trabeculae, that in *Lepidosteus* the pedicle appears very early, and that in Teleosts the palatine process always grows out from the quadrate strongly supports this view, and points to a remote time when neither palatal nor otic processes existed." This opinion is undoubtedly supported by the fact that in *Amia* the quadrate part appears independently and considerably earlier than the pterygo-palatine bridge, the latter remaining at the mesenchymatic stage long after cartilage has developed in the former. Thus during the entire earlier embryonical development it is the quadrate part which is the real suspensorium for the mandibular arch. The hyomandibular connection with the quadrate also appears rather late.

On the hyomandibular (*Hm*) may be distinguished, in addition to the processus symplecticus earlier described, an opercular caudally directed process, which in the earlier stages issues from the central portion of the posterior edge of the hyomandibular in the shape of a broad triangular process. The hyomandibular increases in size during the later stages in a dorso-ventral direction, at the same time undergoing important changes in respect of shape. In the earlier stages it is approximately triangular in form. Later it changes into a rectangular plate, at whose antero-ventral corner the processus symplecticus is sharply defined. The foramen of the nervus hyoideomandibularis, which originally lies nearly in the centre of the hyomandibular, becomes during later development displaced dorsally and somewhat frontad. Of the two remaining, more thoroughly investigated bone ganoids, the hyomandibular in *Lepidosteus* is in the form of a rectangle lying on one of its long sides with its antero-ventral corner prolonged into the greatly extended processus symplecticus, a shape called forth by the special type of cranium in this animal.

In *Polypterus* on the other hand the hyomandibular has a quite different appearance. In a specimen 35 millimetres long, which I had the opportunity of

## THE CRANIAL DEVELOPMENT OF TELEOSTOMIAN FISHES

examining and of which a reconstruction is found in fig. 24, processus symplecticus is completely lacking. The entire cartilaginous hyomandibular (*Hm*) has the form of a narrow cartilage rod, slightly curved and with somewhat expanded lamelliformed ends. In front of this passes the nervus hyoideo-mandibularis. A narrow process, which distally expands into a small lamella is situated somewhat above the middle of the caudal edge of the hyomandibular. On the caudo-lateral part of the latter, united to it by an articular connection is found another eggshaped piece of cartilage which supports the operculum.

With reference to the fact that the hyomandibular is lacking in the fossil Crossopterygians I would make a suggestion, although for the present at least, it cannot be proved, namely that we have before us the rudiment of a stapes, the two chief parts of which, the otostapes and the hyostapes, are here indicated.

It is only at stage 12 that ossifications begin to appear in the cartilage cranium, always in the form of perichondrial lamellæ. The bones of this type, which begin to develop at this stage, are in the neural cranium: the prototicum on the posterior edge of the facial foramen, the occipitale laterale (*Ol*) dorsal to the foramen jugulare, and the basioccipitale (*Bo*) on the ventral side of the occipital region, below and between the foramina jugularia. In the visceral cranium the hyomandibular (*Hm*), the symplectic (*Sy*), the metapterygoid (*Mtp*), the quadrate (*Qu*) and the retroarticular (*Ra*) bones have developed. In the stage of 56 millimetres length, all the chondral bones have begun to appear.

On comparing the three last stages, a peculiarity in the character of the cartilage attracts attention. While stage 11 shows a cartilage of what might be called normal thickness, it is at stage 12 remarkably thin. The cartilage is, in fact, only half as thick in the older stages as in the younger, as has been proved by measurements at many spots of the cranium. The varying thickness depends on difference in development of the intercellular substance. At stage 11 the intercellular substance has the usual transparent appearance, at stage 12 on the other hand it is denser and stains deeper.

The cartilage also appears to contain a greater number of cells. This last circumstance is however only caused by the reduction in quantity of the intercellular substance. As a matter of fact, the cartilage consists of about as many layers of cells as before, although they now lie closer to each other. The cells are rounded, and biscuit-shaped cells are not found. At stage 13 the cartilage is again considerably thicker, about five times as thick as at stage 12, with normally-developed, transparent intercellular substance. The increased thickness is thus caused by the intercellular substance having reformed, but in addition to this an absolute increase in the number of cartilage cells has taken place, which are now to a great extent biscuit-shaped. Thus

at stage 12 the cartilage undergoes, as it were a process of extension, during which the cartilage cranium in general assumes the shape it has in the adult. It is only after this process, that the real growth in size of the cranium takes place, displayed in the following stages as a considerable increase of cartilage, until the cranium finally receives the compact character typical of the full-grown *Amia*.

It is only in connection with this that the development of ridges and bars takes place in the cranium, one result of which is the development of the myodome. The latter is barely indicated even at the 56 millimetres stage.

As previously pointed out, the tip of the notochord already begins to degenerate rather early receding constantly further caudad in the cranium during later development. In order to ascertain whether this regression is absolute or only relative, I have undertaken measurements at different stages of the diameter of the notochord and also of its absolute length, counting from its tip to the frontal edge of the exit of the vagus from the oblongate. The diameter is taken at the foramen glossopharyngei. The result is shown in the following table.

Stage	Diameter c:a	Length mm.
2 .....	0,11	0,66
3 .....	—	—
4 .....	0,11	—
5 .....	0,11	0,69
6 .....	—	—
7 .....	—	—
8 .....	0,13	0,78
9 .....	0,13	0,85
10 .....	0,11	0,92
11 .....	0,10	0,92
12 .....	0,10	0,70
13 .....	—	c:a 0,45

It appears from the second column that the notochord increases within the cranium in absolute length at post-embryonic stages as well, but that it undergoes an absolute regression at the later stages. The figures of the first column point to a circumstance which also appears from the pictures, namely that the notochord, at least during the whole of those stages of development when the cranium is forming, undergoes a relative regression. The growth of the notochord is not in proportion to that of the cranium, but it regresses more and more in a caudal direction. Added to this, there is at stages 12 and 13 an absolute regression resulting in the tip of the notochord lying at the latest stage behind the foramen glossopharyngei. The intercranial part of the notochord thus no longer plays the part of supporting organ.

This circumstance is perhaps not especially remarkable in itself, but is of interest if it be taken into consideration that in *Polypterus* the intercranial part of the notochord undergoes powerful regression, while in *Gasterosteus* (SWINNERTON), the only bony fish in regard to which tolerably exact information exists, the total length increases. The growth of the notochord in the stickleback is, however, also much less rapid than that of the cranium, from which apparent regression results.

It should be pointed out that the parasphenoid in *Polypterus* and in *Amia* extends caudally as far as the first pair of spinal nerves or even somewhat behind the latter, while the same bone in e. g. the adult *Gasterosteus* stops between the foramen glossopharyngei and the foramen jugulare. I have had occasion to observe very strongly pronounced degeneration of the intercranial parts of the notochord in a young *Lepidosteus* of 70 millimetres. The parasphenoid has the same extension in *Lepidosteus* as in *Amia* and *Polypterus*. A long parasphenoid and an intercranially reduced notochord are consequently characteristic of these Ganoids.

The cranium of the Ganoids is generally (GAUPP 1905) described as tropi-basic. LEHN (1918) has now pointed out that *Polypterus* must be regarded as having a typically flat based cranium. This she points out as a remarkable dissimilarity between *Polypterus* on the one hand and *Amia* and *Lepidosteus* on the other. My investigations however show that *Amia*, far from having a typical tropi-basic cranium, must rather be said to be characterized by a pronounced platybasia.

The trabeculae develop at a considerable distance from each other and, although certainly converging slightly frontad, they never give rise to a trabecula communis. The planum orbito-nasale arises only from a cartilage bridge, which unites the tips of the trabeculae and then grows in a rostral and caudal direction. It is true that the cavity of the brain becomes narrower between the eyes, but no interorbital septum develops, in spite of the fact that the eyes, which at the 56 millimetres stage are still on a level with the boundary between the lobi olfacto-ri and the telencephalon proper, have in the adult been displaced still further frontad in regard to the brain. Rostrally the anterior eye-muscle canals are also binary.

In *Lepidosteus* the interorbital septum develops very late. In my 70 millimetres specimen there is still as yet no indication of such a septum, but the eyes are separated by the canal-shaped frontal part of the cavum cerebri, in which run the lobi. From VEIT's reproductions of earlier stages in the development of the primordial cranium it appears further that the trabeculae are not situated as they are in a tropibasic cranium. They converge slightly frontad without however the development of a trabecula communis. In place of the latter, a planum orbito-nasale forms, as in the case of *Amia*, although narrow, in conformity with the shape of the cranium. The cranium is thus

during its embryonal development platy- rather than tropibasic, which was hardly to be expected with regard to the fairly pronounced tropibasia in the adult.

From the above it thus appears that *Polypterus* and *Amia* have a platybasic type of cranium. The cranium of *Lepidosteus* begins as a platybasic, but finally assumes a tropibasic form and might therefore be regarded as primarily platybasic. The platybasia would thus be primitive in the osseous Ganoids.

#### HISTORICAL REMARKS ON THE ORIGIN OF THE DERMAL BONES.

Since KÖLLIKER (1849) accomplished the standard classification of the cranial bones into primordial and dermal bones ("Belegknochen"), these terms have on the whole been maintained. The older histogenetic basis of classification has, however, had to yield to a more topographic one. At the present time the term dermal bones is generally used for bones formed outside the primordial cranium, and the term primordial bones for those, developed from parts of the primordial cranium itself (SCHLEIP, 1904). As a matter of fact, however, not all bones can be assigned to these two categories, as has been also pointed out in the literature (SCHLEIP, GAUPP). Certain bones, for instance the so-called squamosal in the Teleosts or the so-called postfrontal in *Polypterus*, to mention only a few, are compound formations, developing from a membrane bone- and a primordial bone-component (dermo- and auto-component according to VAN WIJHE). Moreover, bones which were originally typical dermal bones, may become more intimately related to the primordial cranium and wholly or in part assume the character of a primordial bone. An instance of this will later be cited in this paper (p. 43), namely the parasphenoid in *Cyclopterus*, which parasphenoid, together with other bones originally looked upon as dermal bones, arises according to UHLMANN (1921) as a typical autostos. UHLMANN himself interprets his observation in another way. He generalizes his results, declaring that most bones arise in connection with the cartilage cranium. This opinion, however, can hardly be correct, since it is founded on observations on a rather specialized bone-fish. The KÖLLIKER classification may, however, be maintained for practical reasons, even though in more specialized forms the distinction between original dermal bones and primordial bones can only be made with the help of comparative anatomy. In any case, the old classification retains its applicability for instance to the Ganoids and in general to all primitive species, recent as well as fossil.

Opinions differ widely in regard to the origin of the dermal bones. HERTWIG (1874) observed in amphibians that certain dermal bones in the mouth

arose through fusion of tooth plates. These observations have since been generalized by HERTWIG and his successors and considered as holding good of all bones in the mouth cavity, an opinion on which, however, great doubts have been expressed. The majority of researches on the development of these bones seems rather to indicate that, in the fishes, the tooth-bearing bones and the teeth arise independently of each other. As it is not my intention in this paper to treat the ontogenesis of these bones in *Amia*, I refrain from expressing any opinion in regard to HERTWIG's theory.

A parallel to HERTWIG's theory regarding the development of the bones in the mouth cavity is GEGENBAUR's theory on the derivation of the dermal bones on the exterior of the cranium. According to GEGENBAUR these bones should be derived from placoid scales like those of the Selachians, their dental part, however, being lost. Since teeth in the mouth cavity and dermal teeth must be regarded as homologous formations, HERTWIG's and GEGENBAUR's opinions may be comprehended in the same theory, namely that all the dermal bones of the cranium have a common origin and are derived from an uniform layer of placoid scales, which is supposed to have existed in the ancestrals of fishes and amphibians. Only the following objection need be raised against this theory that it finds (with the exception of HERTWIG's above-mentioned observations touching certain of the bones in the mouth cavity) no support whatever in the ontogeny.

In regard to the dermal bones which contain sensory canals, VROLIK (1872, p. 276) expressed the following opinion: "Das Frontale und Parietale dienen, insbesondere das Frontale, öfters zur Bergung der sogenannten Schleimkanäle." He based this view especially on his researches in the cranium of the pike, where he found that the sole use of the frontal is to protect the canal system, since the pike has a cartilaginous cranium roof. WALTHER (1887), who also examined the cranium of the pike, declared in opposition to VROLIK that the sensory canals are only secondarily surrounded by bone, but arise primarily as tooth plates. WALTHER bases this opinion chiefly on the development of the dentary, which bone, as in the following will be pointed out, arises in a different way from other canal bones.

VAN WIJHE (1882) uses the relation of the sensory canals to the cranial bones as an argument against the GEGENBAUR-HERTWIG hypothesis, since he discovered that in *Ceratodus* the sensory canals lie above the dermal bones of the head, not under them as they would according to this theory. FÜRBRINGER (1904), it is true, denies the value of VAN WIJHE's argument in its character of a general objection to the tooth plate theory, but on the other hand he establishes the existence in *Ceratodus* of certain bones (sub-mandibular and a number of smaller bones) which have according to him developed in connection with the mandibular sensory canal and with the object of protecting the latter. He points out, however, that in *Ceratodus*

"von einer weitgehenden Beteiligung der Sinneskanalverknöcherung am Aufbau des Craniums keine Rede sein kann" (p. 445).

ALLIS was the first to lay the problem of the sensory canals under detailed investigation in a number of excellent papers. As the most important result of these may be pointed out, firstly the later reviewed account of the development and course of the sensory canals and of the innervation and distribution of the sensory organs, secondly "that a bone or part of a bone developed in any particular fish in relation to a particular part of the lateral-line system is always the homologue of the bone, or of the part of a bone, developed in relation to the same part of the lateral-line system in any other fish or animal" (1898, p. 430).

It should, however, be pointed out in this connection that SAGEMEHL (1884) already called attention to the relation of the sensory canals to the bones, "da diese Beziehungen sehr konstante sind und in fraglichen Fällen zur Bestimmung zweifelhafter Homologien benutzt werden können" (p. 182).

On the origin of the sensory canal bones ALLIS writes (1889) that in young larvae where the bones are just beginning to develop, they are represented by short semi-cylindrical pieces lying immediately below each organ. This opinion does not wholly tally with my results, for, as I will later point out, bones primarily belonging to two or more canal organs develop in several places. ALLIS further considers that the cranial bones which contain sensory canals have a double origin and are formed from a canal bone component, giving rise only to the canal bone proper, and a component from which the cranial bone proper develop. This opinion has also been put forward earlier from different quarters. Thus SCHMID-MONNARD (1883) found that in *Salmo* and *Esox*, while that part of the squamosal directly surrounding the sensory canal is formed from particular osteoblasts, the other parts of this bone, develops as a membranous ossification only secondarily fusing with the sensory canal bone. McMURRICH (1884) described the development of the sensory canal bones in *Ameiurus* in the same way. ALLIS considers that these observations agree with his in regard to *Amia*. "The frontal for example, in 20 millimetres larvae of *Amia*, consists of two wholly separate parts, a cylindrical gutter lying immediately beneath the supra-orbital canal, and a flat, plate-like portion lying mesial to the canal, directly upon the cartilage of the chondrocranium" (1898, p. 428). ALLIS considered that this opinion of his on the double origin of the sensory canal bones, was confirmed by SAGEMEHL's observations in *Citharinus* (1885), according to which the canal bones proper lie on the surface of the cranial bones or even in certain Teleosts as a special bone cylinder system, completely divided from the cranium proper. SAGEMEHL supposed that it was a question of secondary conditions in these extreme cases, which ALLIS consequently denies.

KLAATSCII (1894) propounded the theory that the scleroblasts might be

derived from the ectoderm. He distinguished between two kinds of dermal bones, those derived from the dermal sensory organs and those originating in the environment of the teeth rudiments. According to KLAATSCH, the sensory canal bones would thus have a single origin. His statements in regard to the ectodermal extraction of the dermal bones has not, however, been corroborated by later investigators. SCHLEIP (1904) has investigated the same material as that on which KLAATSCH based his results, namely *Salmo*, with the intention of controlling his theory, and found that (p. 416) "weder an den von KLAATSCH bezeichneten Stellen, noch an irgendwelchen anderen Orten beim Lachs und der Forelle irgendein Befund zu erheben ist, aus welchem man eine ektodermale Herkunft der Skleroblasten schliessen kann".

With regard to the origin of the canal-bearing bones in Salmon, SCHLEIP has arrived at the same result as I have done in the case of *Amia*.

It may finally be mentioned that UHLMANN in a lately published work (1921) states that the embodiment of the canals in the bones is of a secondary nature.

As may be seen from the above summary account, very widely differing views are to be found in the literature in regard to the origin of the dermal bones. This may partly be explained by the fact that such very varying material has formed the basis for these views. But even those research-workers who have had identical material for their investigations, have come to very varying results, as e. g. SCHMID-MONNARD on the one hand, and SCHLEIP on the other, *Salmo* being the object for their investigations. This contradiction may, however, likewise be explained by the latter having commenced his investigations on considerably younger specimens than the former, and thus been able to trace the development of the bones from the beginning.

In respect of ALLIS's statement on the origin of frontal, it may be pointed out, that he has not described either frontal or the other bones in detail, a task lying outside the scope of his real object in the work.

#### THE DEVELOPMENT OF BONES RELATED TO SENSORY CANALS.

The cranial sensory canals in *Amia* have, ever since BRIDGE (1877) gave a fairly correct description of their course, repeatedly been objects of research. BRIDGE's statements were corroborated by VAN WIJHE (1882) and SAGEMEHL (1884). These scientists pointed out the fixed course of the canals and their relation to certain bones in the cranium. It is, however, above all ALLIS, who in a number of excellent works has given detailed investigation to the morphological significance of the sensory canals as well as to their development and anatomy.

In the following short orientation on the development, structure and

course of the canals, I follow in the main ALLIS' principal work on the canal system in *Amia* (1889), referring to this work for all details.

In the canal system may be distinguished on each side of the head the infra-orbital line, the supra-orbital line and the preopercular-mandibular line. To these may be added the single supra-temporal commissura (fig. 16).

The infra-orbital canal is a direct continuation of the main lateral line of the body. It diverges behind the eye ventrally running downward and forward below the eye to the ethmoidal region, where it rounds the anterior nasal aperture on the outer side and unites with the canal from the opposite side on the tip of the nose between the nasal tubes. In bony fishes the pre-nasal part is lacking. It exists on the other hand both in *Polypterus*, *Lepidosteus* and in many fossil Teleostomes. The supra-orbital canal begins somewhat medially and behind the nasal tubes and runs caudad above the eye, uniting behind the latter with the infra-orbital canal. The preoperculo-mandibular line begins near the tip of the lower jaw, but without uniting the canal on the opposite side. It runs caudad along the lower edge of the mandible almost to its posterior end, where it curves first upwards and then sharply caudad, after which it runs upwards in a curve following the preoperculum. After leaving the upper end of this bone it unites with the infra-orbital canal. It is originally formed from a mandibular and a preopercular part, which unite into a canal. In e. g. *Esox* the two components remain distinct also in the adult. The supra-temporal commissure rises in the caudal portion of the temporal region from a canal coming from each of the infra-orbital canals. They unite in the middle line into a single connection.

The canals contain a number of sensory organs, which always occur in a fixed number for each species. In *Amia* they may be divided into six groups with regard to their innervation, each group of which is ontogenetically derived from a particular rudiment which gives rise not only to the sense-organs but also to their nerves. These groups are:

1. The first 16 organs in the infra-orbital canal, which together with the sensory organ in the spiracular canal are innervated by the Ramus buccalis and the Ramus oticus of the nervus facialis.
2. The 7 organs in the supra-orbital canal, which are innervated by the Ramus ophthalmicus facialis.
3. The 16 organs in the operculo-mandibular line, which are innervated by the Ramus mandibularis externus facialis.
4. Organ 17 in the infra-orbital line, which is innervated by the dorsal branch of the N. glossopharyngeus.
5. Organs 18 and 19 in the infra-orbital canal, and the three organs in the supra-temporal canal, which are innervated by the vagus.

6. Organ 20 and 21 in the infra-orbital line, which together with the organs in the main lateral line on the body are innervated by *N. lineae lateralis* of the vagus.

With regard to the innervation of the sensory canals EWART (1892) and others assign to the infra-orbital canal only those parts which are innervated from the *facialis* system. According to this point of view, which I also hold, those parts of the canal containing organs 17—21, and also the supra-temporal commissura, should be assigned to the cranial section of the main lateral line.

In addition to the organs enclosed in the canals there are still two kinds of cutaneous sensory organs in *Amia*, namely the pit organs described by ALLIS, which, similarly to the canal organs, are disposed in lines, and the organs called by MERKEL terminal buds, of which great numbers are irregularly distributed in the skin on the different parts of the head. The former constitute seven shorter lines on either side (fig. 16), three of which lie dorsal to the infra-orbital line and the cranial prolongation of the lateral line. The three first-mentioned lines are: the anterior head line, lying immediately behind the junction of the infra- and the supra-orbital canals, the posterior head line in front of the supra-temporal commissure and the middle head line between the two others. Of the remaining four a horizontal line of cheek lies behind the eye between the infra-orbital and the opercular canal, a vertical line at right angles to and below the latter, a mandibular line above the angular bone and a gular line on the gular plate. These lines are innervated by the same nerves as the adjoining canal organs. MERKEL's terminal buds are innervated by the trigeminus, whose *Rami ophthalmici* and *superior maxillary* branches are chiefly used for this purpose.

In this connection it may be pointed out that ALLIS, whose description I have here followed in the main, has found in *Salvelinus* (1889), *Esox*, *Salmo* and *Silurus* (1905), a line of sensory organs lying in the epidermis on the tip of the nose in the same region where the ethmoidal commissure is situated in *Amia*. He has moreover established the existence of other similar lines, corresponding to those above-mentioned in *Amia*. It might thus be supposed that pit lines and sensory canals are morphologically related organs, all the more so as they are innervated from the same place. The transverse ethmoidal line in *Salvelinus* etc. should thus be homologous with the ethmoidal commissure in *Amia*, although representing another phylogenetic stage. In accordance with this, the pit lines in *Amia* might be explained as rudimentary formations representing canals which existed in phylogenetically older forms. ALLIS has himself (1905) with regard to the development of the canals in *Plagiostomes* on the one hand, *Teleosts* and *Ganoidei holostei* on the other, distinguished between two types of canals, the *plagiostomian* canal and the *teleostean* canal. He points out as his opinion that "both of these canals must

be derived from some common earlier condition of the system, which is apparently represented in the pit lines of *Amia*".

From STENSIÖ's description (1921) of the triassic fishes he has collected in Spitzbergen, it appears that the Crossopterygians as well as other older Teleostomes show in the arrangement of both the canal system and the pit lines, conditions which may be interpreted in accordance with what has been stated above. Thus, STENSIÖ says of the Cœlacanthids described by him: "In the posterior part of the lacrymo-jugal or immediately dorsal of this a canal issues in a backward and downward arch from the post-orbital section of the infra-orbital canal." This canal, called by him the jugal canal, corresponds to a similarly situated canal in the Stegocephals. According to his pictures, this canal occupies the identical position as that of the horizontal cheek line in *Amia*.

The conditions in the fossil Crossopterygians might in consequence be thus described: the preopercular canal curves cranially towards the post-orbital part of the infra-orbital canal (fig. 23), while in the recent Teleostomes (figs. 16 and 24) it unites with the latter at its juncture with the cranial section of the main lateral line. STENSIÖ cannot from his material determine whether it anastomoses with the mandibular canal, a circumstance which does not, however, affect the correctness of this interpretation.

ALLIS has (1889) given a detailed description of the ontogenesis of the sensory canals in *Amia*. But previously to this, their development in *Cottus* has been described by BODENSTEIN (1882) in a more summary manner but showing that the sensory canals principally arise in the same way as in *Amia*.

At younger stages each of the canal organs lies at the bottom of a little pit. These pits become united by a faintly delineated groove. Lip-shaped formations develop from the edges of the pits, parallel with the longitudinal axis of the future canal, meeting above the sensory organ, they thus form a short, tunnel-like formation over each organ. Thus the canals arise as a line of rather short pieces, one to each canal organ, their orifices approaching each other as the canal pieces increase in length. The canal pieces do not as a rule become completely fused, but their orifices unite forming the primary pores. In regard to the complications which arise on certain points through the uniting of primary pores I must refer to the work of ALLIS. The primary pores in *Amia* and *Lepidosteus* lose during the later stages of their development their tube-like shape, and form through repeated subdivision a widely ramified net-work of canals, opening on the skin through smaller secondary pores. This does not occur in *Polypterus*.

In the following description of the development of the bones related to the sensory canals I make use for the present of the terminology of ALLIS (and SAGEMEHL).

Bones developing in connection with the anterior part of the infra-orbital canal.

The infra-orbital canal and the cranial part of the lateral line pass through the ethmoid, ant-orbital, lacrymal, supra-orbitals I and II, post-orbitals I and II, post-frontal, squamosal, extrascapular and suprascapular (figs. 16 and 17).

In the *Amia* of 10.6 millimetres length the infra-orbital canal behind the ethmoidal commissure is only indicated as a shallow groove, becoming more and more flattened out caudad in the supra-orbital region. The canal organs are, however, already developed. The ethmoidal commissure is somewhat in advance of the other parts in development. The epithelium which is to form the future canal is easily distinguished from its environment by its greater height. Owing to this circumstance the rudiment of the canal may be observed even where there is as yet no indication of a groove. The epithelium is generally by a basal membrane divided from the underlying connective tissue — as yet only a sparsely nucleated mesenchyma. The basal membrane under the canal organs is more powerfully developed than elsewhere. At this early stage it may be observed that the connective-tissue cells lie somewhat more closely packed under the canal rudiment, especially in its immediate proximity, although in many places as yet only in a single layer. The layer of connective-tissue cells is more closely packed and higher under the anterior part of the canal rudiment. It was not possible to discover whether these cells — the osteoblasts — are derived from the epithelium, but it seemed improbable.

In the *Amia* of 12 millimetres length the aggregations of osteoblasts have withdrawn somewhat from the epithelium, surrounding a thin structureless membrane of bone tissue.

*Ethmoid* (figs. 15, 16 and 17).

Together with the ethmoidal commissure, which is still groove-shaped, four distinct groups of osteoblasts (fig. 15) may be distinguished in the 12 millimetres *Amia*. They develop behind each of the four canal organs (1 and 2 in the infra-orbital line on either side).

The groups of osteoblasts surround the canal rudiment from behind like a gutter and lie rather far laterad, two on each side in connection with

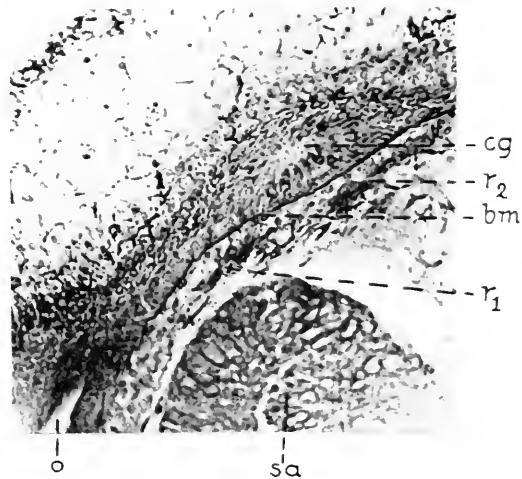


Fig. 15. *Amia calva*, Stage 8. Transvers section passing through the ethmoidal commissure (left half).

*bm*, basal membrane; *cg*, epithelium of the canal rudiment; *o*, future lateral tube; *r*<sub>1</sub> and *r*<sub>2</sub>, lateral osteoblastic rudiments of the ethmoid; *sa*, sucking apparatus. Micr. phot.

the canal organs. There are consequently as yet no osteoblasts round the median part of the canal. In 14 millimetres *Amia* the canal is closed but still lacks osteoblasts rostrally. On the other hand a layer of osteoblasts in conjunction with the central part has now developed, containing a bone lamella and connected with the inner of the lateral rudiments described in the previous stage. The median layer stretches farther rostral on the ventral than on the dorsal side. The rostral sections of the two lateral parts still preserve their independence, but have fused caudally, behind the canal. As the canal at this point suddenly curves frontad, the dorsal and the ventral lamelle of each rudiment unite here for a short distance. These bone rudiments have on the cross sections of this part the appearance of a horizontal X, whose lateral shanks are the dorsal and ventral lamelle of the most lateral rudiment, while the median shanks have arisen in a similar way from the inner of the two lateral rudiments. The median bone rudiment, which, as I have previously mentioned, was already from the beginning united with its right and left neighbours, has on its caudal side an incisure exactly in the middle line. This part of the ethmoid extends farther caudad than the side parts. As a whole, the ethmoid consequently has the shape of a bone gutter open frontad and provided with an incisure in the middle line (in the sagittal plane) and a constriction on each side.

In the 33 millimetres *Amia* (fig. 17) the previously gutter-shaped bone has closed up into a cylinder, and at the 56 millimetres stage its final shape has in the main developed. At this later stage the lateral parts of the ethmoid lie immediately above the premaxillaria and the centre above the rostrum. It has however preserved its cylindrical shape. It has on its posterior section only a small median, caudally directed solid process lying embedded in the connective tissue over the rostrum.

Consequently the ethmoid in *Amia* does not develop as a single bone, but seems to consist of four lateral rudiments and possibly one median, which in its turn may contain two rudiments.

STENSIÖ (1921) has examined a number of unusually well-preserved triassic fishes collected by him in Spitzbergen, belonging partly to the Crossopterygians, partly to other older teleostome groups. The sensory canals, which are distinctly developed in his material, have to a large extent rendered homologizing of these formations possible. I therefore gladly avail myself of and follow STENSIÖ's excellent work in the main for my comparisons of fossil forms.

STENSIÖ points out that the ethmoid in *Amia* evidently corresponds to "the middle rostral in *Colobodus* and a couple of median rostrals in primitive Rhipidistids". The latter (figs. 22 and 23) had 2 to 4 median and 2 lateral rostrals, which are all traversed by the ethmoidal commissure of the sensory canal. In the somewhat younger *Colobodus*, the middle rostrals have become

fused into a single bone. STENSIÖ considers that this middle rostral corresponds to the ethmoid of *Amia*, the homologue of the binary lateral rostral having fused with the antorbital. He therefore proposes the name of "middle rostral" for the ethmoid in *Amia*. From my researches in *Amia* it seems however more probable that the so-called ethmoid corresponds to the middle rostral of *Colobodus* together with the lateral rostrals and might consequently be called simply "rostral", which name I suggest instead of STENSIÖ's "middle rostral".

STENSIÖ finds it impossible to prove with any certainty whether this bone also includes elements corresponding to the inter-rostrals of the Cross-ptyergians, although considering the extension of the bone caudad between the nasals he thinks this probable. The correctness of this view is upheld, it seems to me, by the conditions in the embryonic stage, where the median part of the ethmoidal rudiment and the sensory canal lie more caudally than the lateral sections.

The arguments which have been brought forward in regard to *Amia*, probably hold good also in regard to *Polypterus*, where the so-called ethmoid corresponds as to position with the conditions in *Amia* (cf. ALLIS 1900 b and STENSIÖ 1921).

STENSIÖ has also suggested that the homologue of the rostral may be found in the ethmoid of the Teleosts. He considers it "very probable that at least in such forms as *Elops* and possibly even in *Salmo*, *Silurus* and *Esox* the anterior part of the so-called mesethmoid is homologous to the middle rostrals in *Colobodus* or one or more of the medial rostral elements of the Rhipidistids".

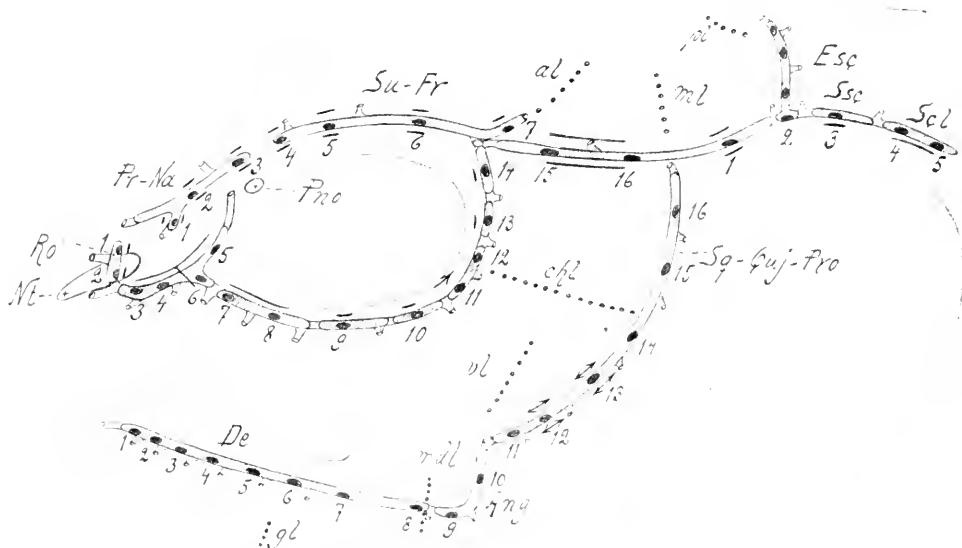
As has already been mentioned, the Teleosts lack an ethmoidal commissure of the infra-orbital canal. But according to ALLIS there is in the forms enumerated by STENSIÖ a pit line situated above the anterior part of the mesethmoid.

As has previously been pointed out, this pit line may be considered as having the same morphological value for the homologizing of skeletal elements as the sensory canals themselves. Thus, the frontal part of the ethmoid of these bony fishes may at any rate be considered homologous with the ethmoid in *Amia*, i. e. with the rostrals. In *Salmo* and some other bony fishes the ethmoid develops as a dermal ossification, while in others it appears as a typical primordial bone. The question thus arises whether this bone is homologous with the dermal one. The following argument may, it appears to me, give the solution. UHLMANN (1921) has described the development of the cranium in *Cyclopterus* and found that most bones, also those which are generally regarded as dermal, develop as primordial bones. A dermal bone, confidently homologized through the whole of the fish series as the parasphenoid, nevertheless begins its development according to UHL-

MANN as a typical autostos. In spite of this it seems highly improbable that the paraspheoid in this fish should be considered as anything other than the similarly denominated bone in e. g. *Salmo* or *Esox*. Hence it follows that a bone, which in certain (primitive) species forms as a dermal bone, may very well, owing to later acquired more intimate relations with the cartilage cranium, develop embryologically as a cartilage bone. I consequently consider that the circumstance of the ethmoid being in certain species a typical primordial bone cannot form a hindrance for homologizing it with rostral bones. Of course I presuppose that no other obstacles of a comparative anatomical nature arise.

*Intorbital, lacrymal, sub- and post-orbital bones. Postfrontal* (figs. 16, 17 and 18).

Close to the pre-orbital section of the rudiment of the infra-orbital canal, two isolated groups of osteoblasts may be distinguished in the 12 millimetres



stage. Each group contains a thin, gutter-shaped bone lamella lying under the rudiment of the sensory canal, separated from the latter only by a narrow mesenchymatic layer (cf. fig. 18). These two bone rudiments represent the antorbital and the lacrymal.

The earliest development of these as well as of the other bones containing sensory canals agrees perfectly with SCHLEIP's description (1904) of the corresponding process in *Salmo*. A cross section of the lacrymal or the antorbital rudiment at this stage has the same appearance as SCHLEIP's picture of the frontal in a trout of 16 millimetres length.

The lacrymal commences developing in a single piece in conjunction with canal organs 7 and 8. Above the rudiment of the antorbital the sensory canal sends out a dorsally directed, pre-orbital branch, containing canal organ 5. In front of this branch, which has already closed into a canal, lie canal organs 3 and 4, and behind it organ 6 (fig. 16). The antorbital rudiment lying along the sensory canal, will therefore consist of a longer, horizontal, and a shorter, vertical branch (cf. ALLIS 1889, fig. 42). Similarly to the lacrymal it develops, however, as a single piece.

In 14 millimetres *Amia* new bone rudiments have appeared caudally to the former. In addition to the two bones, which have previously begun to develop, there are now indications of the supraorbitals I and II in connection with the canal organs 9 and 10 respectively, and the anterior part of the postorbital I (figs. 16 and 18). The latter bone later contains two organs (11 and 12). Under 11 the aggregation of osteoblasts has approximately the same appearance as those lying in front of it, that is, it lies at some distance from the epithelium in the shape of a thin, curved plate, containing an extremely thin bone lamella. The bone ends somewhat behind organ 11. At the same time the aggregation of osteoblasts draws closer to the epithelium becoming gradually thinner the further back one goes in the serie. It continues finally in the shape of a single layer of cells close beneath the epithelium under organ 12. Under organ 13, later situated in the postorbital II, a more compact aggregation of osteoblasts is again found, which becomes thinner caudally. The formation of bone begins consequently in those parts of the mesenchyma lying under the sense organs, but not so that an aggregation of osteoblasts, or a point of ossification, appears under each separate canal organ.

At the 19.5 millimetres stage the rudiment of the postorbital I has increased in size in a caudal direction forming a gutter-shaped bone under canal-organs 11 and 12. Thus this bone now completely agrees in appearance with the lacrymal at the previous stage.

Under organ 13 appears the rudiment of postorbital II and somewhat dorsally to organ 14 the rudiment of the postfrontal.

In the next stages, all the above enumerated bones retain their gutter-form, although deepening more and more in consequence of the growth of

the edges of the bones in the direction of the skin. It is only at stage 12 (fig. 17) that they finally close up into cylinders, the walls of which are, however, perforated to allow the passage of nerves, blood-vessels and the tubes through which the canals open on the surface of the skin. Such tubes are generally found between each of the bones in the orbital arch. They also appear, moreover, between each particular canal organ in the bones, containing more than one sensory organ, a circumstance explained by the ontogenesis of the canal (cf. page 40).

Already at stage 6 small aliform lamellae are to be seen on the lacrymal and the postorbitals, extending parallel to the above lying skin. These lamellae

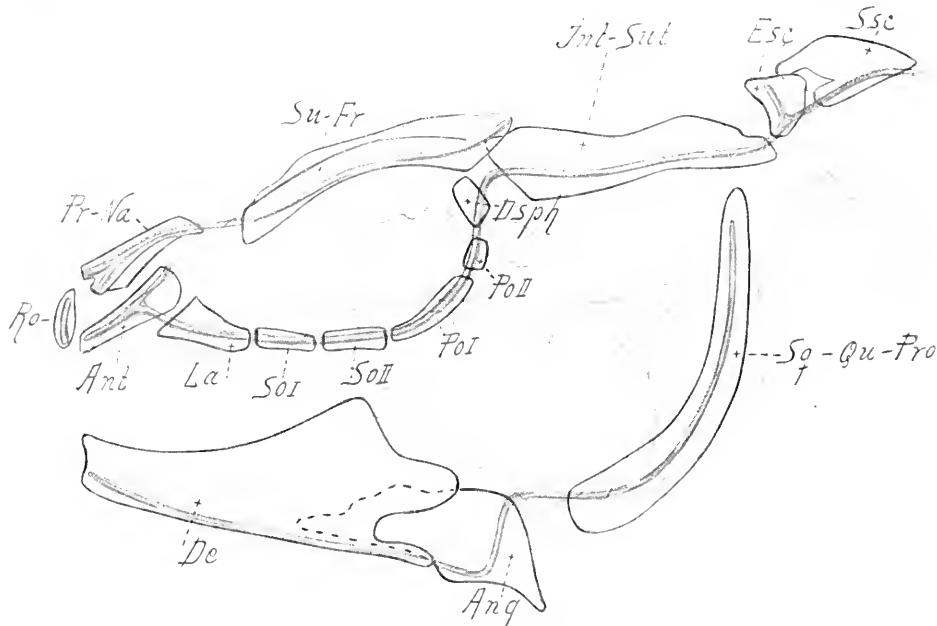


Fig. 17. *Amia calva*. Stage 12. Lateral view of the crane, showing the canal bones. The sensory canals (slightly schematic) are indicated by shading. Tubes and pores are not drawn. *Ang*, angular; *Ant*, anorbital; *De*, dentary; *Dsph*, dermosphenotic; *Esc*, extrascapular; *Int-Sut*, intertemporo-supratemporal squamosal; *La*, lacrymal; *Po I* and *Po II*, postorbitals; *Pr-Va*, postrostral-nasal (nasal); *Ro*, rostral (ethmoid); *So I* and *So II*, suborbitals; *Sq-Qu-Pro*, squamoso-quadratojugal preopercular (preopercular); *Ssc*, suprascapular; *Su-Fr*, supraorbital-frontal (frontal). Outlines of the primordial crane indicated by thin lines (cf. fig. 14).

develop continuously from the canal bones and are thus mere processes of the latter. I wish to draw attention to this circumstance already at this point (cf. fig. 19).

In 56 millimetres *Amia* the bones have on the whole assumed their final form. The suborbitals are thus single, cylindrical bones, while the others, the postorbitals in particular owing to the vigorous growth of their lamellae, have extended far over the original area. The lamellae are, however, still quite thin and appear distinctly as processes from the cylindrical canal section.

As already mentioned, the development of these bones begins similarly to that in *Salmo*. The orbitals 2—6 in BÖKER's (1913) model of a 33 millimetres *Salmo* agree altogether in appearance and disposition with the corresponding bones in *Amia* at stage 12 (fig. 17). The orbital 1 is not, however, in *Salmo* connected with the infra-orbital canal and develops, according to SCHLEIP, as an ossification from an aggregation of cells in the roof of the nasal saccule. Unfortunately there is no information in regard to the number and distribution of the canal organs in the orbitals, which renders the attempts at homologizing the individual elements more difficult. Whether the orbital 1 is possibly homologous with the antorbital in *Amia* is a question I am at present unable to answer. The divergence of their development need not prove an obstacle for this homologizing, when we recollect the varying course of the sensory canal and what has been stated above in regard to the ethmoid.

The so-called postfrontal, which should more correctly be denoted by the name of dermosphenotic introduced by PARKE, completes the orbital arch of the infra-orbitals. It only begins to develop at stage 10 (19,5 millimetres) as an aggregation of osteoblasts in connection with canal organ 14, though somewhat dorsal to the latter. At the next stage bone has developed in the osteoblasts rudiment, which develops in the same way as the above-mentioned bones. The dermosphenotic does not occupy any special position in relation to these bones, except that it is situated close to the cartilage cranium, where it lies immediately lateral to the post-orbital part, on the spot where a perichondral ossification, the autosphenotic, is formed in the 56 millimetres *Amia*. SAGEMEHL (1884) found these two elements fused into a single formation, whereas ALLIS, who also examined a number of fullgrown specimens, has always found them independent. According to ALLIS (1905) it is only in *Polypterus* that they invariably fuse. This fusion evidently takes place very early, for in a 35 millimetres specimen of this animal the two components are already so completely fused that no boundary can be observed between them.

In *Polypterus*, the infra-orbital elements which lie rostrally to the sphenotic also show divergent conditions, which has already been pointed out by ALLIS (1900 b) amongst others. The bone which in *Amia* corresponds to the antorbital forms part of the so-called premaxillary and is tooth-bearing. The so-called maxillary consists of a palatine part, which according to ALLIS is

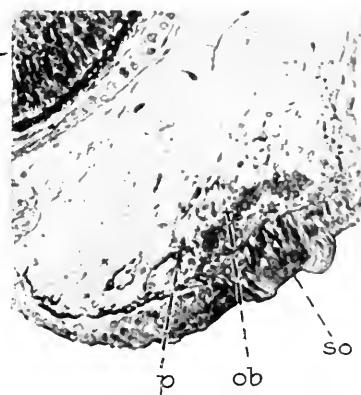


Fig. 18. *Amia calva*. Stage 9. Osteoblastic rudiment of suborbital I. Cross-section. Micr. phot.  
e, eye; ob, gutter-formed osteoblastic rudiment; p, pigment; so, sense organ (infraorb. 9).

homologous with the dermopalatine in *Amia* and the Teleosts, and another part corresponding to sub- and post-orbital elements (fig. 24), which is also tooth-bearing. The caudal prolongation of this canal section of the maxillary forms in my 35 millimetres specimen a process, which passes inside the anterior edge of the checkplate. The form and position of the canal part of the maxillary recall the conditions in the Coelacanthid *Wimania*, STENSIÖ (fig. 23), to which I will come back when describing the development of the preoperculum.

Bones developing in connection with the dorsal parts  
of the sensory canal-system.

*Nasal and frontal.*

The pairy nasals and frontals arise in connection with the supra-orbital canal. The nasal develops under the supra-orbital organs 1, 2 and 3 in the following manner (cf. fig. 19). In 12 millimetres *Amia* a faintly indicated concentration of mesenchymatic cells may be distinguished beneath the sensory canal, which is still groove-shaped. Under organ 2, these cells have arranged themselves in two somewhat elongated aggregations of osteoblasts parallel with the canal rudiment. In other specimens of the same stage, but somewhat more advanced, aggregations of osteoblasts could also be observed under the organs 1 and 3, although no binarity was as yet visible in these rudiments. In somewhat older specimens (14 millimetres),

the anterior rudiment (under organ 1) has assumed about the same form as that lying under organ 2 at the preceding stage.

That part of the now completed canal round which rudiment Nr. 1 forms, does not run in the same direction as the caudal part of the canal. It begins with a lateral pore, running thence inwards and then deviating caudad. Canal-organs 2 and 3 together with the rudiments of bone which have developed in connection with them are situated in the posterior longitudinal section,

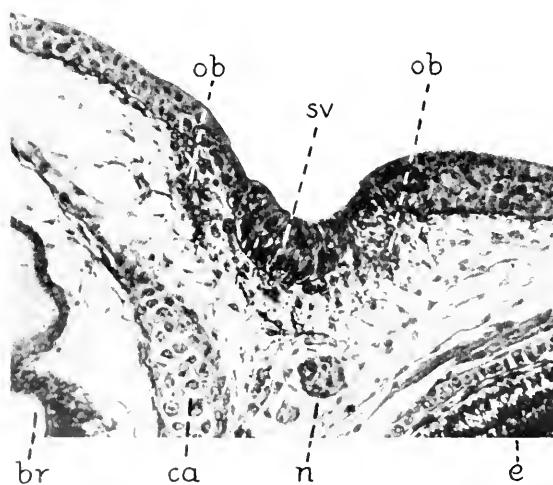


Fig. 19 *Amia calva*. A series of cross-sections of the rudiment of the frontal at different stages of development. Micr. phot.  
a. Stage 8.

*br*, brain; *ca*, cartilage (parenchymoidal); *e*, eye; *n*, ramus ophthalmicus facialis; *ob*, pairy osteoblastic rudiments; *sv*, canal organ nr 6 supraorb.

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Nr. 1 in the anterior transversal section. In consequence of this, the now binary osteoblast groups in the latter rudiment lie one more rostrally, the other further caudally. The anterior part of osteoblast group Nr. 2 has already become fused into a single rudiment, in which a bone lamella is formed, showing the typical gutter form, characteristic of a young sensory canal bone. The caudal part of the bone rudiment is, however, cleft into two tips, i. e. the fusion of the binary rudiment runs from the front caudad. Between organs Nr. 2 and 3 the two tips narrow till they can only be traced as a few solitary osteoblasts under the canal. Under organ 3 an osteoblast aggregation is again found, containing a thin bone lamella. This rudiment can not be proved binary at this stage. At the next stage (19,5 mm.) the rudiments have all become fused to a single bone gutter. The caudal end of the latter, which is formed from bone rudiment Nr. 3, increases continually in a caudal direction, showing the characteristic subdivision into two tips, indicative of its binary origin. At still later stages the gutter is converted into a cylinder, which through the development from its sides of lamellas in the manner previously described by degrees assumes the form of the future bone. The original canal is through the greater part of the bone situated approximately in the median line, but further laterally in the caudal part. The above described development of the nasal bone differs on two important points from the origin of other bones

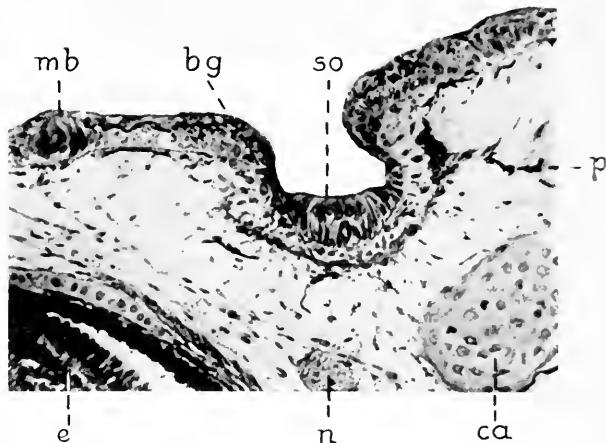


Fig. 19 b. Stage 9.

*bg*, bony gutter, rights, at the pigment-cell (*p*) a developing lamelliformed process; *ca*, cartilage; *e*, eye; *mb*, Merkel's terminal bud; *so*, supraorb. sense organ 6.

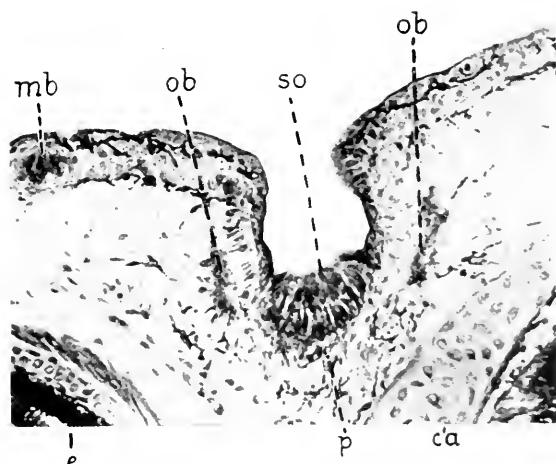


Fig. 19 c. The same stage as in b. but showing a section through canal organ 5.

*ob*, airy tips of the bone rudiment; *so*, sense organ 5. Other letters as in b.

with several sense-organs. For example, while the antorbital arises in one piece and the development of the postorbital progresses continuously from the first-formed osteoblast aggregation, the nasal takes its origin discontinuously, i. e. from several different spots almost simultaneously. The first-formed osteoblast centra are moreover binary.

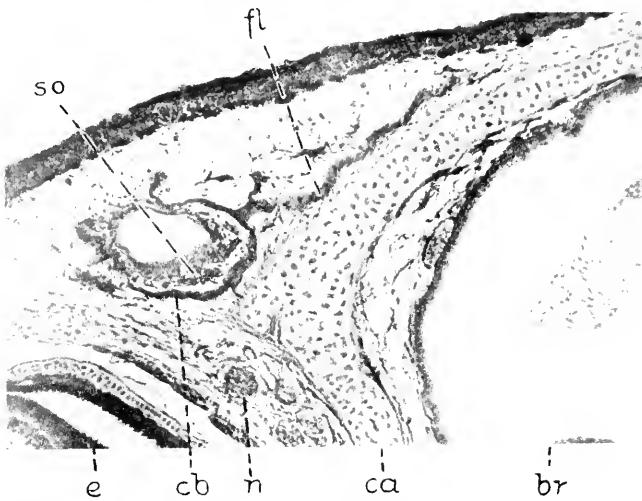


Fig. 19 d. Stage 11.

*br*, brain; *ca*, cartilage; *cb*, canal bone; *e*, eye; *fl*, medially directed frontal lamella; *so*, sense organ 6.

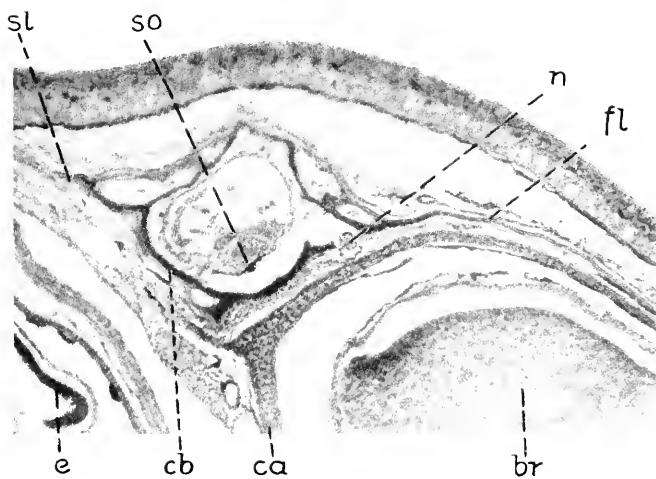


Fig. 19 e. Stage 12.

*br*, brain; *ca*, cartilage; *cb*, canal bone; *e*, eye; *fl*, frontal lamella; *n*, nerve, passing through a foramen in the bone; *sl*, supraorbital lamella; *so*, sense organ 6.

It appears from this that the nasal may be considered as formed from three different units, the origin of each of which is in its turn binary. The

conditions of the supraorbital canal in *Polypterus* are similar to those in *Amia* both in regard to its course and to the number of its sense-organs, a fact already pointed out by ALLIS (1900) and which I have had opportunity of controlling in my 3.5 cm. specimen. *Polypterus* has however three different bones in the rostral part of the supraorbital canal, the so-called *os terminale*, accessory nasal and nasal. Each of these contains but one sense-organ. The striking agreement on the question of the relation of the bones to the sensory canal, caused ALLIS to state that: "The agreement is so exact that it clearly establishes the homology of the three bones in the one fish with the single one in the other." The above description of the development furnishes the conclusory proof for this statement. BRIDGE (1888) has moreover found in one of the two specimens he has investigated the two first bones represented by a single one, which thus shows an intermediate stage of the conditions in *Amia*. The Rhipidistid *Dictyonosteus* (fig. 21) was also provided with three nasals on each side. As the supraorbital canal in this case ran into the ethmoidal commissure, it held a straighter course and the three bones were situated in line behind each other. The homology with the *os nasale* of *Amia* is nevertheless evident. The significance of the binarity of the rudiments will be treated later.

The frontals arise similarly in the main to the nasals, and in connection with the four following supraorbital organs 4—7. At the 12 mm. stage, when the canal has still only the form of a gutter, binary osteoblast aggregations are formed under the organs 4, 5 and 6 (figs. 16 and 19). The last-mentioned is considerably ahead of the others in development; bone-lamellas early develop in it, which fuse, forming a gutter, the process of ossification then continuing in a rostral direction. The tip of the growing gutter-shaped bone is however always binary (fig. 19). The whole bone-rudiment (with the exception of the most rostral part) is at these early stages situated above the *taenia marginalis*. The rostral and the caudal parts of the bone-gutter approximate fairly closely to the cartilage. The caudal part of the frontal develops rather late. As late as the 21.5 mm. stage no osteoblast aggregation can be distinguished under canal organ 7. A gap in the material between stages 21.5 and 31.5 mm. has unfortunately prevented me from following the development of this part in detail. At the 21.5 mm. stage the lateral lamellæ have begun to develop. It appears from fig. 20 that the latter are rather narrow laterally and broader medially. The shape of the bone at this stage shows that the development of the frontal process proper is more rapid between the tubes of the sensory canal; this circumstance may possibly point to its origin from several seriatly disposed rudiments. At stage 12 each frontal forms a single bone, which meets its *vis-à-vis* on the central line (fig. 17). From the postero-lateral corner of each frontal projects a caudally directed process. Above the latter

lies canal organ 7. This process is consequently the latest developed part of the frontal.

Like the nasal, each frontal develops from clearly binary rudiments (with a possible exception in the case of the caudal part). These binary rudiments moreover exhibit a seriate disposition.

As already mentioned (page 25) there still remains in *Amia* at the 19.5 mm. stage, when the rostral fontanelle of the primordial cranium has become covered, a foramen, which from inside becomes filled by the epi-

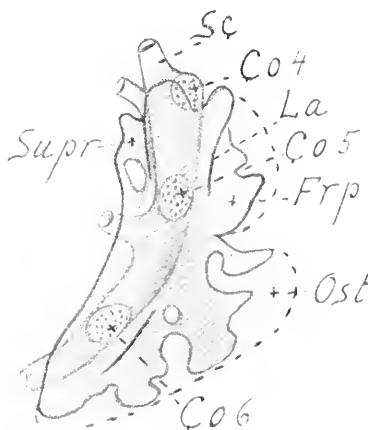


Fig. 20. *Amia calva*. Stage 11. Ventral view of the left frontal bone ( $50 \times 1$ ). *Co4*—*Co6*, supraorbital canal organs 4—6; *FTP*, frontal lamella of the canal bone; *La*, perpendicular lamella (margin of the bone gutter); *Ost*, osteoblastic layer; *Sc*, sensory canal; *Supr*, supraorbital lamella.

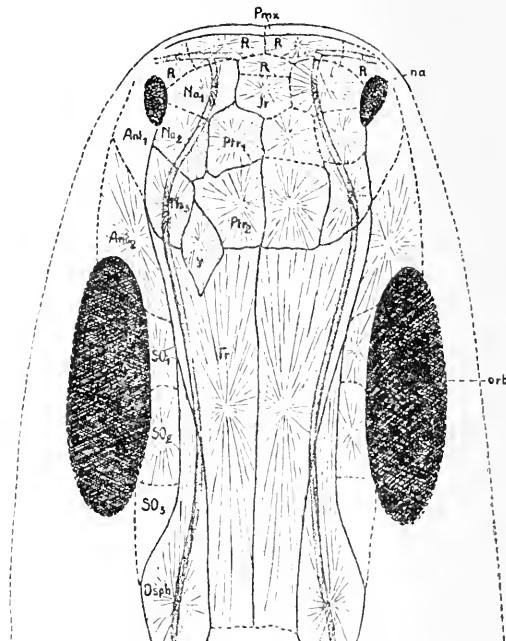


Fig. 21. *Dictyonosteus artecius* STENSTÖ. The anterior part of the cranial roof. Sensory canals with dotted lines and shading. From STENSTÖ.)

*Ant1* and *Ant2*, anorbital elements; *Dsph*, dermosphenoticum; *Fr*, frontal; *Ir*, interrostral; *Nas*, nasal elements; *Pmx*, premaxillary; *Ptr1* and *Ptr2*, postrostral elements; *R*, rostral; *So*, supraorbitals; *na*, nasal aperture; *orb*, orbita; *y*, accessory boneplate.

physis. At this stage when the frontals are already beginning to develop, this foramen may be seen to lie approximately on a level with the caudal third part of the existing frontal rudiment. This circumstance seems to me to be of great interest. It is namely well-known that the older Crossopterygians e. g. *Osteolepis* (WATSON and DAY 1916) had a so-called "parietal foramen" situated exactly between the two frontals. I suggest naming this foramen, which is clearly homologous with the corresponding formation in *Amia*, foramen epiphyseos, as being a more adequate term.

Another significant fact in regard to the earlier development of the

supraorbital bones in *Amia* is, that each bone is not only segmented originally in a transversal but also in a longitudinal direction. These circumstances point, as has already been emphasized in regard to the nasal, to the conditions in the fossil Crossopterygians and other older Teleostomes. It might be said that in *Amia* bones form on either side of the sensory canal which bones later fuse into single pieces — the definitive bones in this fish. The supraorbital sensory canal in the Crossopterygians often runs between two rows of bones instead of inside the same. This is e. g. the case in the Rhipidistid *Dictyonosteus* described by STENSIÖ (fig. 21), where the supraorbitals are found alongside the frontal. These three supraorbitals correspond to the three lateral aggregations of osteoblasts under the canal organs 4, 5 and 6 in *Amia*-embryos. This appears still more clearly in the Cœlacanthid *Axelia* STENSIÖ. The conditions in my 35 mm. *Polypterus* bear me up in this conception. The frontal is here cloven below the sensory canal, with the exception of its caudal part, and consists consequently of a narrower lateral and a broader median part. The former corresponds with the supraorbital row in *Dictyonosteus* or with the single supraorbital in *Eusthenopteron* (fig. 22), the latter part being the frontal proper.

In regard to the homologons of the binary nasal rudiments, it is possible that they may be recognized partly in the above-mentioned three nasals of *Dictyonosteus*, partly in the postrostrals and perhaps in the interrostral in the same fish. The former answer to the lateral elements of the *Amia*-embryo, the latter to the median. It seems to me that the enigmatic mosaic arrangement of the bones of the cranial roof in the older Teleostomes might be explained in this manner.

In accordance with what has been previously stated, the nasal in *Amia* ought to be termed *nasale-postrostrale*, a bone which, as already mentioned, corresponds with the three nasal elements in *Polypterus*. The frontal is a *supraorbitale-frontale* in both *Polypterus* and *Amia*.

*Squamosal bone.*

In the temporal continuation of the infraorbital canal, immediately caudal to the dermosphenotic begins the formation of the so-called squamosal bone. Various authors, — I refer amongst others to STENSIÖ (1921) — have pointed out the unsuitability of this term for a bone belonging to the infraorbital canal. The squamosal of Stegocephalians, which should be considered homologous with the squamosal of other Tetrapods, belongs, namely, to the preopercular canal. In Stegocephalians as in the fossil Crossopterygians this canal does not anastomose with the temporal but with the postorbital part of the infraorbital canal (comp. figs. 23 and 24 and page 40).

The earliest development of the squamosal of *Amia* proceeds in the main on the same lines as that above described in respect of the nasal and frontal.

In the adult the squamosal contains the infraorbital sense-organs 15 and 16 as well as the organ 1 in the main lateral line.

In the 14 mm. *Amia* on each side of the sensory canal groove, paired bone-rudiments are present below the canal organ 15. In a more advanced specimen may be observed that these paired rudiments have grown caudad as to reach the canal organ 16. No indication of fusion between the two rudiments is to be seen. The groove-shaped rudiment of the canal gradually ceases behind organ 16; it may only be noticed that in its caudal prolongation the epithelium is somewhat higher than that of the environment. It is only further caudad that a groove-shaped depression appears, in which lies the above-mentioned canal organ 1. It is easily seen and appears also from fig. 16 that this organ is situated behind the spot where the preopercular, the infraorbital and the main lateral lines meet. The entire rudiment of the squamosal lies immediately above the crista parotica. Under organ 1 a bone-lamella first appears at the 19,5 mm. stage in *Amia*, when the two rostral elements have already fused to a single bone and sent out a rather broad median lamella. It is only at stage 12 that the rostral and caudal parts of the bone become united. At this stage, however, that part of the canal proper lying between the canal organ 16 and 1, consists of an open groove. This shows that canal organ 1 with its bones occupies a rather independent position in the so-called squamosal. This also appears from the fact that this canal organ and the middle head line of pits is innervated by *nervus glossopharyngeus*, organs 15 and 16 on the other hand by *nervus facialis*. The so-called squamosal contains in consequence at least two different elements, a rostral and a caudal. For the moment I pass over the fact that these two elements are binary; it will be touched on later.

ALLIS (1919) has homologized the squamosal in *Amia* with the supratemporal and intertemporal in *Osteolepis macrolepidotus* described by GOODRICH (1919). According to ALLIS, they correspond with the caudal and rostral part of the squamosal of *Amia*; "the one doubtless representing that part of the laterosensory canal that is innervated by the supratemporal branch of the glossopharyngeus, and the other the part innervated by the ramus oticus lateralis". ALLIS' conception is strikingly confirmed by my observations. *Eusthenopteron* (fig. 22) completely corresponds in this respect with *Osteolepis*.

Similarly to *Amia*, *Eusthenopteron* had a parietal which was not connected with the sensory canal. I consider it not improbably that this parietal in *Eusthenopteron* was a product of the sensory canal, and thus answered to the inner binary rudiments of the intertemporal-supratemporal in *Amia*, the outer giving rise to the intertemporal-supratemporal proper. The part of the canal in question would thus be analogous with that part of the supraorbital canal lying in front of it, which laterally throws off the supraorbitals,

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medially the frontal. The so-called parietal in *Amia* and the Teleosts, which originates in the form of an ossification in a membrane, would thus be a new formation and not homologous with the parietal in *Eusthenopteron*.

*Polypterus* has, as is well-known, a so-called squamoso-parietale (ALLIS, 1900) i. e. the supraorbital sensory canal runs in the lateral border of each parietal. The postero-lateral part of this bone contains an organ of sense, which like organ 1 in *Amia*, is innervated by the glossopharyngeus. The entire lateral part is consequently homologous with the intertemporal-supratemporal in *Amia*. This bone doubtless however also contains the homologon to the parietal in *Eusthenopteron*, and ought therefore to be a parieto-intertemporo-supratemporal. STENSIÖ describes in the Cœlacanthids *Axelia* and *Wimania* a parieto-intertemporal. Postero-lateral to it lies a bone traversed by the main sensory canal. In the caudal part of the bone the canal anastomoses with the supratemporal-commissure. The bone contains thus the most lateral element in the extra-scapular row. STENSIÖ calls this bone supratemporo-extrascapulare. The supratemporal part of this bone must in consequence of its position be considered homologous with the supratemporal part in e. g. *Amia* and *Polypterus*, described in the compound bone supratemporal-intertemporal.

The extrascapulars in *Amia* form rather late, and consists of a bone on either side containing 4 canal organs apiece, viz. organ 2 from the main lateral line besides 3 commissure organs. The above-mentioned gap in my material has unhappily prevented my following the development of these bones. The first rudiment

appears only at stage 11 (21.5 mm.) in the form of an osteoblast aggregation under the most laterally situated of the commissure-organs, and at my next stage (31.5—34.5 mm.) a single bone has already developed. It is probable that each extrascapular originates from three, possibly four different bone-rudiments. ALLIS has shown in a most convincing manner that the three so-called supratemporals found on either side in *Polypterus* must be homologous with the single extrascapular of *Amia*. In the above-mentioned Cœlacanthide *Axelia* three extrascapulars on either side were found in addition to the lateral supratemporo-extrascapular. These additional extrascapulars are consequently in accordance with the greatest number of rudiments which

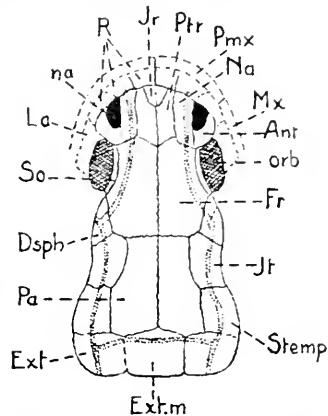


Fig. 22. *Eusthenopteron fordii* WHITEAVES. Cranial roof (from STENSIÖ).

*Ant*, antorbital; *Ext* and *Ext.m*, extrascapulars; *Fr*, frontal; *It*, intertemporal; *La*, lacrimal; *Mx*, maxillary; *Na*, nasal; *Pta*, parietal; *Pmx*, premaxillary; *Psr*, postrostral; *R*, rostrals; *So*, supraorbital; *Stemp*, supratemporal; *na*, nasal aperture; *orb*, orbit.

could theoretically be the source of Amia's extrascapular, if one bone-rudiment arises in conjunction with each sense-organ in the commissure.

Behind the supratemporal-commissure the suprascapular forms in conjunction with organ 3 and the supracleithral in conjunction with canal organs 4 and 5. These two originate in the same way as e. g. the antorbital and begin to form earlier than the extrascapulars.

Bones developing in connection with the mandibular-preopercular canal.

*Preopercular bone.*

In the mandibular-preopercular sensory canal the two components form at rather different periods. While the mandibular part of the canal closes already at stage 9, this process takes place only at stage 10 in the preopercular part. At stage 12 the two canals are still united only by a groove above the quadrate joint.

At stage 9 the rudiment of the preopercular part of the canal can only be observed as an epithelial band, differing from its environment by its height. In this rudiment lie the canal organs 11—16 (mand.-preop.). Under organs 12 and 13 bone-rudiments may already be found (fig. 16). That belonging to Nr. 13 consists of two small bone plates, one lying more rostrally, the other more caudally. The greater part of the rudiment under Nr. 12 is cloven; it proved, however, difficult to decide whether this was a case of two quite separate rudiments.

Already at the next stage the different bone nuclei have become fused to a single piece of bone, which in the form of a bone gutter extends along the whole of the now complete canal. At stage 12 the gutter has closed in a tube, furnished with low lamella-like processes, and has now in the main the form exhibited by the fully developed bone (fig. 17). My presentation of the development of preoperculum is also somewhat imperfect, owing to the relatively late development of this bone. It is thus impossible for me positively to determine whether isolated bone-rudiments also occur in connection with canal organs 14—16. It seems to me, however, that judging by the appearance of the bone at stage 10, this were hardly the case.

The development of preoperculum is of especial interest, because my observations, in spite of the above-mentioned imperfections, might contribute to the solution of the squamosal-question in the recent Teleostomes. As previously stated, the bone which should rightly be called squamosal, i. e. the homologon to the squamosal of Stegocephalians, is a canal bone, traversed by the jugal canal (comp. page 53). In certain older Teleostomes e. g. *Wimania* (fig. 23) two bones connected with this canal were found, one ventrally, the quadrato-jugal, and one dorsally, the squamioso-preopercular. *Watson* and

DAY (1916) illustrate in *Glyptopomus* three cheek-plates, viz. a ventral bone, with they call quadrato-jugale, and two dorsal bones, the caudal being the preoperculum and the rostral the squamosal. The conditions are similar in *Holoptychius* (WATSON and DAY). The homologons in *Wimania* to these two latter bones are consequently fused into the single squamoso-preopercular. It appears highly probable that in the earliest bone-rudiments of *Amia* homologons to the above-mentioned bones may be traced. The binary bone-rudiment under organ 13 answers respectively to the preopercular and the squamosal, the bone-rudiment under organ 12 to the quadrato-jugal(-preopercular). In consequence the homologons to the squamosal should only be found in the

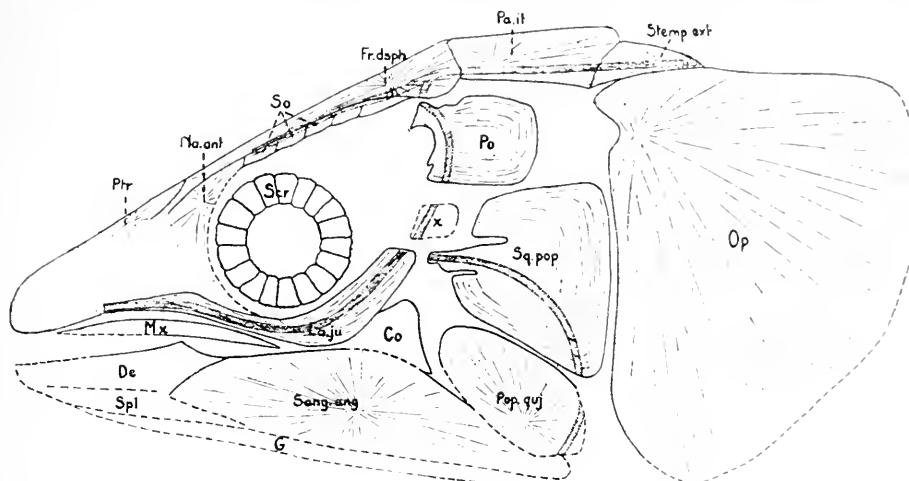


Fig. 23. *Wimania sinuosa* STENSIÖ. Lateral view of the head. Sensory canals with dotted lines and shading. (From STENSIÖ.)

*Co*, coronoid; *De*, dental; *Fr.dsph*, fronto dermosphenotic; *G*, gular plate; *Laju*, lacrymo-jugal; *Mx*, maxillary; *Na.ant*, nasalo antorbital; *Op*, operculum; *Pa.it*, parieto-intertemporal; *Po*, postorbital; *Pop.guj*, preoperculo-quadratojugal; *Ptr*, postrostral; *Sang.ang*, supraangulo-angular; *Ser*, sclerotic plates; *So*, supraorbitals; *Spl*, splenial; *Sq.pop*, squamoso-preopercular; *Stemp ext*, supraretemporo-extrascapular; *x*, jugal plate.

so-called preopercular. This probably holds good, not only for *Amia*, but also for the Teleosts. ALLIS (1919) considers that squamosal elements are represented in the posterior portions of the two postorbitals. This view is in no way supported by the ontogeny of the bones in question. As has already been pointed out in the foregoing statements, the postorbitals originate as typical canal bones. Their large caudally directed processes are simply lamella-like processes, which have arisen in the usual manner from that part of the earliest formed bones in which the sensory canal runs.

In 35 millimetres *Polypterus* (fig. 24) the preoperculum consists of a narrower ventral portion and a wider dorsal part. From the latter a small rostral process projects, which is partly covered by the caudal process from the postorbital portion of the so-called maxillary. The entire dorsal portion, as well

in regard to position as form, is so strikingly reminiscent of squamoso-preopercular in *Wimania* (fig. 23), that the homology presents itself unsought. It is true that squamoso-preopercular in *Wimania* contains the jugal canal, while the sensory canal in *Polypterus* follows the course usual in the recent Teleostomes, but with regard to the fact that it is replaced by the morphologically equivalent cheek line of pits (comp. page 39) this circumstance ought to prove no hindrance for the homology. The dorsal portion of preoperculum in *Polypterus* would consequently be homologous with the squamoso-preopercular, and the ventral with the quadrato-jugal-preopercular. TRAQUAIR (1881) has in *Rhizodopsis*, a species agreeing with *Glyptopomus* in regard to

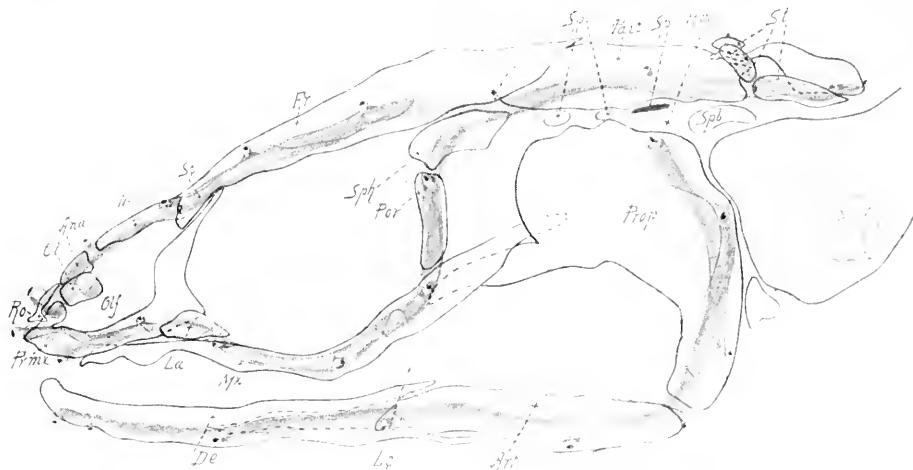


Fig. 24. *Polypterus bichir*, 35 mm. total length. Lateral view of the crane, showing the sensory canals and canal bones. Outlines of the primordial crane indicated by thin lines.

*Ana*, accessory nasal; *Art*, angular; *De*, dentary; *Fr*, supraorbital-frontal (frontal); *Hm*, hyomandibular; *La*, lacrymal; *Lc*, labial cartilage; *Mx*, maxillary; *Na*, nasal; *Or*, os terminale; *Off*, nasal aperture; *Pait*, parieto-intertemporo supratemporal (parietal); *Por*, postorbital; *Prmx*, premaxillary; *Prop*, squamoso-quadrato-jugal-preopercular (preopercular); *Ro*, rostral (ethmoid); *Sc*, sensory canal; *Sp*, spiracular aperture; *Sph*, dermosphenotic; *St*, extra-scapulars supratemporals).

the development of the cheek plates, homologized the preopercular and squamosal with the whole of the preoperculum in *Polypterus*. TRAQUAIR considers the ventral cheek plate (quadrato-jugal) in *Rhizodopsis* homologous with bone *y''* in his descriptions of *Polypterus* (1870). It seems to me hardly probable, however, that this should be the case. Firstly, bone *y''* is not related to any sensory canal, and secondly, it develops very late. It is still lacking in 35 millimetres *Polypterus*, though all canal bones are developed at this stage. In this respect it recalls the only category of dermal bones still for the most part lacking at this stage, namely the spiracular row of bones.

#### *Dentary and angular bones (figs. 16 and 17).*

These two bones, which are related to the mandibular canal, do not develop in precisely the same way as the other sensory canal bones. SCHLEIP

has (1904) already made the same observations in regard to the dentary in *Salmo*. The more complicated development of these bones is assuredly connected with the fact that they are early called upon to support teeth. They become hereby exposed to functional influences, which change the course their development would otherwise have taken. In other words, the ontogeny does not follow phylogenetic lines.

I therefore restrict myself to a brief report of my observations. Already in stage 6 the dentary has begun to develop in the shape of an elongated slightly gutter-formed bone lying along the Meckelian cartilage. Its frontal end lies close to the cartilage, but caudad it diverges more from the latter. This bone is not yet in any way connected with the sensory canal, of which only the sensory organs lying in the epithelium can be observed. Its dorsal parts become at least topographically connected with teeth rudiments.

At the next stage, a beginning development of osteoblasts may be observed in relation to the canal organs 7 and 8. At a somewhat later stage bone has developed in this rudiment. This bone, however, appears immediately to fuse with the dentary. A similar independent bone rudiment seems to develop in relation to the canal organs 2 and 3, but also fuses with the dentary as soon as bone has had time to develop. Both rudiments appear binary.

At stage 9 the dentary is a fair-sized bone, which apparently consists, partly of a tooth-bearing component lying close to the Meckelian cartilage, partly of a canal component, fused with the former. Caudally, the bone is cleft in two branches, a dorsal, which lies along the processus coronoideus and is a process from the dental bone-component, and a ventral, situated in the caudal continuation of the sensory canal. SCHLEIP, who has observed the same conditions in *Salmo*, suggests that the dentary may have arisen from a canal component and a dentary-bone.

In the mandibular line are found ten sense organs, of which the first eight are included in the canal section of the dentary and the last two in the angular (ALLIS, 1889, gives the number as seven and three).

In connection with the last two canal organs, no bone has as yet developed as late as at stage 9. There is, however, close to the posterior part of the Meckelian cartilage and inside of the caudal end of the dentary a triangular, dermal ossification, the angular. In 21.5 millimetres *Amia* we find on the latter perpendicular lamellæ, which will act as canal bones related to that part of the canal containing the sense organs 9 and 10.

It thus appears as though the dentary and the angular consist either of a canal part and another component, or possibly, like the angular, are secondarily related to the sensory canal.

My opinion is, however, that neither of these alternatives is correct but that there is a third possibility, namely, that the first developed plates respectively of the dentary and the angular in *Amia* are phylogenetically

products of the sensory canal in the same way as e. g. the frontal. In *Polypterus* (fig. 24) the bones in question are undoubtedly sensory canal bones, on which the teeth are directly fastened. I cannot, however, put forward any proof for this opinion, but restrict myself to a surmise. A study of the earliest bone development in *Polypterus* would certainly throw light on the problem.

#### GENERAL RESULTS.

As the result of my investigations of the development of the bones related to sensory canals in *Amia*, I beg to point out the following:

The first rudiment of these bones develop in connection with the sense organs in the canals, pass through a gutter-shaped stage, close up into bone-cylinders, containing the canal, after which the bone receives its definite shape through the development from these bone-cylinders of lamelliform processes. The definitive bone is thus a product of the original canal-covering. This conception is based on direct observations.

Every canal bone, by which term I understand the entire bone that develops in relation to the canal has developed phylogenetically as a covering for the sense organs enclosed within the canal. It is possible that in this case a bone rudiment (two on the dorsal side of the head), originally developed round each sense organ, in much the same manner as is still the case in the main body line, where each sense organ is protected by a scaly covering. In accordance with this, it may be imagined that the canal organs of the head were likewise protected by formations possibly derived from placoid scales, although not assuming with GEGENBAUR, that every membrane-bone is formed from a large complex of fused basal plates.

My conception of the phylogenetic connection between the canal bones and the sensory canal is based on the fact that the canal bones play a very important role in all the primitive Teleostomes, fossil as well as recent. In *Chimæra* (RUUD 1917) the canals are surrounded by horseshoe-shaped pieces of bone, which, with the teeth, are the only ossifications in this primitive animal. In more specialized fishes the connection between the canals and the cranial bones may dissolve, by which the former would lie in a secondary position above the cranium proper, either unprotected or imperfectly surrounded by bones. Embryological investigations of these forms are much to be desired.

In *Amia* the canal bones develop in a manner, which makes direct homology with the canal bones in the oldest Teleostomes possible (Crossopterygians, *Dipterus*). Whether the great agreement between the latter and the embryonic stages of *Amia* can be said to hint at a primitive organization in this fish, is a question which is unanswerable till similar morphogenetic investigations

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of the development of the cranium in other fishes have been carried out. Such investigations are especially desirable in regard to *Polypterus* and primitive Teleosts (*Salmonides*, *Clupeides*, *Siluroides*).

Certain features in the ontogeny of the primordial cranium point to primitive relations in *Amia*. Such features are the presence of independent supra-orbital cartilages and the development of a frontal foramen epiphyseos.

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